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Plankton dynamics in a temperate estuary with observations on a variable hydrographic condition

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PLANKTON DYNAMICS IN A TEMPERATE ESTUARY

WITH

OBSERVATIONS ON A VARIABLE HYDROGRAPHIC CONDITION

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APPROVAL SHEET

This dissertation is submitted in partial fulfillment

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DEDICATION

This work is dedicated to my parents Mr. and Mrs. Herman Haas in appreciation for their continued encouragement and support throughout my education.

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PREFACE

This thesis consists of three manuscripts with a common introduction and conclusion plus appendices. The first manuscript concerns hydrographic aspects of the lower York River and lower Chesapeake Bay area, and has been approved for submission to Estuarine and Coastal Marine Science. The second manuscript concerns aspects of phytoplankton dynamics in the lower York River and was written in anticipation of submission to Limnology and Oceanography. The third manuscript is approved for submission to Archives of Microbiology, and concerns the nutritional mode of cultured non-pigmented microflagellates isolated from the lower York River. The appendices present salinity and tide data for the lower York and Rappahannock Rivers for 1974, and biological and environmental data from the phytoplankton study in the lower York River.

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Above all else I am grateful to Betsy. Without her optimism, encouragement, help and love for seven long years this achievement would be only a distant dream.

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NUTRITIONAL MODE OF SEVERAL NON-PIGMENTED MICROFLAGELLATES FROM THE YORK RIVER ESTUARY, VIRGINIA

ABSTRACT

A station in the York River mouth (37°14'40" N. lat., 76° 23'28" W. long., depth ca. 18 meters) was occupied eight times (24-36 hours duration) during 1974 for the purpose of elucidating 1. the hydrographic characteristics, and 2. the dynamics of the phytoplankton community of this temperate estuarine system. Emphasis in the phytoplankton study centered on defining the role of the nannoplankton (<15μm) and the short term (hourly) variation in plankton parameters. Temperature, salinity, dissolved oxygen, light penetration, chlorophyll a (Chl a), and in situ primary production (PP) were measured at intervals through the water column periodically for the duration of each station.

The hydrographic data indicated that this estuary oscillated between conditions of considerable vertical salinity stratification and homogeneity on a cycle that was closely correlated with the neap and spring tides respectively. As a result of the annual cycle in the magnitude of the spring tides, periods of homogeneity were more pronounced in late summer than in winter. Variation in freshwater flow appeared to have little effect on the hydrography. The results support the contention that the hydrographic characteristics of the major subestuaries of the lower Chesapeake Bay and possibly the lower Bay proper are regulated primarily by tidally related factors rather than freshwater inflow.

The nannoplankton accounted for 65-90% of the total Chl a and PP during each station except February (55% Chl a and 19% PP) and May (44% Chl a and 37% PP). Nannoplankton influence appeared to peak in late summer. Maximum daily Chl a levels ranged from 5-25 μg l^{-1} with no apparent seasonal trend. A diel variation was observed in Chl a abundance with highest concentrations at mid afternoon and lowest concentrations at midnight to 0300. The daily increase in nannoplankton Chl a generally doubled the minimum daily concentration. Plots of assimilation ratio (μg C hr^{-1}μg Chl a^{-1}) versus in situ light intensity for both the total and nannoplankton resembled typical photosynthesis versus light intensity curves (i.e. hyperbolic) with no inhibition observed at light levels up to 0.6 langleys min^{-1}. A diel variation was observed in assimilation ratios with highest values in the afternoon on short and medium length days and high morning and afternoon values separated by a noontime depression on long days. Light saturated assimilation ratios (Pmax) were generally correlated with temperature. However, Pmax values in July and August were reduced to 50% of the June values (at comparable temperatures) presumably a result of shade adaptation associated with a surface mixed layer 5-6 times deeper than the euphotic zone. High Pmax values for the net plankton (> 15 μm) in February were presumed to be due to temporal succession of a cold adapted

species. The results suggest that a highly dynamic nannoplankton community exists in this estuary, possibly doubling every 24 hours but with biomass accumulations limited by grazing. It is proposed that a close coupling exists between zooplankton grazing, ammonia excretion and phytoplankton ammonia assimilation.

Five species of non-pigmented microflagellates (5-8 μm in diameter) were isolated from the lower York River and grown in culture. Despite their obligately heterotrophic nature, none were capable of assimilating a variety of simple organic compounds. They all demonstrated a marked capacity for ingesting high numbers of bacteria. The results indicate that non-pigmented microflagellates apparently do not compete with bacteria for dissolved organic matter but may be an important pathway for the reentry of bacterial biomass into the food web.

PLANKTON DYNAMICS IN A TEMPERATE ESTUARY

WITH

OBSERVATIONS ON A VARIABLE HYDROGRAPHIC CONDITION

INTRODUCTION

With the twin pressures of increasing population and industrial development, man's impingement on and alteration of estuaries grows daily. Sewage treatment plants introduce organic and inorganic nutrients to the water. Power plants introduce heated water. Industries add materials with actual or potential toxic effects. New channels are dredged and bordering marshlands are filled, altering flow characteristics and turbidity. As a result of these alterations, scientists are increasingly called upon to predict the effect of such impingements on the indigenous biota. These predictions are based on the assumption (implicit or explicit) that we understand the functional dynamics of the estuarine ecosystem - that we recognize the significant biotic components, know their rates of production and utilization, how they interact and how they are controlled. Unfortunately, our basic understanding of the dynamics of energy flow and nutrient flux in the lower trophic levels of most estuarine systems is not sufficient for a meaningful predictive capability.

This lack of understanding is primarily the result of the extreme complexity of temperate estuarine ecosystems. To a large extent, successful field work on plankton dynamics has been performed in oceanic environments that are more amenable to interpretation such as the Sargasso Sea (Menzel, Hulbert and Ryther, 1963), or the central gyre of North Pacific (Eppley, Renger, Venrick and Mullin, 1973).

These plankton ecosystems are characterized by reduced numbers of trophic levels, relatively simplified energy flows and environmental conditions (temperature, salinity, light, nutrients, hydrography) that persist nearly unchanged for long periods of time. As a result, biological interactions and controlling factors are in a relatively steady-state equilibrium, facilitating their analysis and interpretation.

This is not the case in a temperate estuary like the lower Chesapeake Bay and its tributaries. In these plankton ecosystems additional trophic levels become significant (i.e. secondary carnivores and decomposers) and the species diversity in each trophic level is rich. As a result, pathways of energy flow are highly fragmented resulting in both a complex food web and a greater potential for regulation. Biological investigations are further complicated by species succession within the net phytoplankton (Manzi, 1973; Mackiernan, 1968) and the net zooplankton (G. C. Grant, personal communication) that occurs throughout the year. Each new species has its own inherent response to light, temperature, nutrients and susceptability to grazing. The potentially patchy distribution of the phytoplankton (Cassie, 1963; Wiebe and Holland, 1968) is further complicated by tidal excursions up to seven kilometers per tidal cycle which convert spatial variation into temporal variation when sampling at a fixed point over time. The possibility of diel variations in the magnitude of measured parameters further complicates the sampling procedure and interpretation of results.

In such complex ecosystems, possible controlling factors are not as obvious. The multiplicity of potential phytoplankton grazers (fish, micro- and net zooplankton, planktonic larvae, benthic inverte-

brates) complicates the assessment of this potential regulatory mechanism. Nutrients may enter the ecosystem via freshwater river input (derived either from natural weathering processes or agricultural activity), from the salt marshes bordering the estuary, from the sediments, from higher salinity ocean water, or most likely be regenerated within the euphotic zone. Nutrient sinks are equally diversified and include phytoplankton, bacteria, the salt marshes and sediments as well as transport out of the estuary.

Physical environmental conditions (climatic and hydrographic) in the York River estuary are equally complex. Both salinity and temperature vary widely during the year. Freshwater influx varies seasonally as well as over the longer (drought years versus wet years) and shorter (hurricans Agnes and Camille) term. The waters of the lower York River vary between extremes of vertical salinity stratification and homogeneity over time periods measured in days (personal observation) and the forces that regulate these hydrographic conditions are not known.

The degree of vertical salinity stratification may have a significant effect on phytoplankton abundance. The occurrence of phytoplankton blooms coincident with highly stratified water columns has been demonstrated for coastal waters (Gran and Braarud, 1935; Sverdrup, 1953), estuaries (Welch, 1969; Welch et al., 1972) and fjords (Gilmartin, 1964). In addition to promoting phytoplankton blooms, a highly stratified condition may reduce the flux of nutrients between the euphotic zone and the deep waters and/or sediments. The degree of vertical stratification might also be expected to have an effect on the physiological status of the phytoplankton. For example, in oceanic

ecosystems phytoplankton from below the surface mixed layer have been shown to be shade adapted compared to the phytoplankton maintained within the euphotic zone (Steemann-Nielsen and Hansen, 1959).

Elucidating the functional dynamics of such an estuarine ecosystem, though difficult, may not be impossible. It does, however, call for a particular analytical approach. It is apparent that even with unlimited resources, all possible species-species and species-environment interactions cannot be catalogued much less analyzed. Consequently, one must attempt to overcome the complexity of the real ecosystem by identifying and compartmentalizing only the dominant (in terms of energy flow, nutrient cycling or control capability) components at each trophic level. Available information should serve as a guide as to what the significant areas of research might be (e.g. National Academy of Sciences, 1975). Secondly, one should stress the functional rather than only the structural aspects of the ecosystem. Rates of flow or interaction between compartments should be emphasized over merely the standing stock at any given time. One approach to analyzing interactions between biotic components and the biotic and abiotic components is to examine short term changes (i.e. hourly) that may occur in selected parameters within the ecosystem. With this knowledge one can postulate the types of interactions that account for these variations and subsequently experimentally test the prediction.

This approach to ecosystem analysis differs from that utilized by many previous investigations of the plankton community of the lower Chesapeake Bay. Previous studies stressed primarily the structural aspects of the plankton community (i.e. how many of a particular species

or how much of a particular chemical component) without adequate attention to its functional significance. For example, Stofan (1973) and Manzi (1973) enumerated the large dinoflagellates and diatoms (i.e. the net phytoplankton) respectively of the lower York River, even though available evidence indicated that the very small phytoplankton (the nannoplankton) dominated primary production. Previous phytoplankton studies determined the nitrate concentration of the water. Evidence now suggests that Chesapeake Bay phytoplankton preferentially utilize nitrogen from urea and ammonia rather than nitrate. Previous studies of phytoplankton dynamics in this environment were limited to one sample per day (Warinner and Zubkoff, 1973; Patten, Mulford and Warinner, 1963), precluding any analysis of cause and effect relationships between short term variations in plankton parameters. Analysis of long term (i.e. weekly or monthly) cause and effect relationships is difficult in a dynamic ecosystem such as the lower York River because of the extreme biotic and hydrographic variation that can occur in a relatively short time period.

A summary of relatively recent investigations of estuarine plankton communities suggest that the flow of carbon and nutrients through the lower trophic levels of the lower Chesapeake Bay plankton community may follow a pattern similar to the compartmental model in Figure 1. The bracketed numbers in the following text indicate pathways designated in Figure 1.

The domination of most marine phytoplankton communities by the nannoplankton (ca. 10-20 μm effective diameter) is now well established (Pomeroy, 1974). Earlier phytoplankton studies in the mid and lower Chesapeake Bay indicated the possible significance of the nanno-

plankton to the total primary productivity of the area (Mackiernan, 1968; Marshall, 1967; Patten et al., 1963), and two recent studies have documented their significance (McCarthy, Taylor and Loftus, 1974; VanValkenburg and Flemer, 1974). Very little is known concerning species composition or species succession of the nannoplankton, but available evidence suggests that they are comprised primarily of phytoflagellates rather than diatoms and dinoflagellates (Boney, 1970; Campbell, 1973).

Because of their small size and different susceptability to grazing compared to the netplankton, the nannoplankton dominance may result in presently unsuspected pathways of energy flow (Malone, 1971; Parsons and LeBrasseur, 1970; Ryther, 1969). For example, protozoans such ciliates, rotifers and tintinnids (i.e. the micro-zooplankton) may be the dominant grazers of the nannoplankton (1a) (Beers and Stewart, 1969; Parsons and LeBrasseur, 1970; Pomeroy, 1975; Pomeroy and Johannes, 1968). It is also known that net zooplankton such as *Acartia sp.* prey on the nannoplankton (1b) (Storms and Taylor, 1973). The nannoplankton are also known to be the principal food of the planktonic larvae of both benthic molluscs (Knight-Jones, 1950; Gross, 1937) and fish (Subrahmanyan and Sarma, 1965).

A recent study of nitrogen utilization by Chesapeake Bay phytoplankton (McCarthy and Taylor, 1974) indicated that the rapidly recycled forms of nitrogen such as urea and ammonia rather than nitrate were preferentially utilized by the phytoplankton (3a). This is logical since the nitrogen from ammonia and urea can be directly incorporated into cellular material while nitrate nitrogen must first be reduced, an energy requiring process. The production of urea and ammonia pro-

bably results primarily from animal excretion (2a, 2b) (Johannes, 1968; Pomeroy, 1970; 1975; Pomeroy et al., 1972). Considering the inherently higher metabolic rate of the microzooplankton (a consequence of their smaller size and larger surface area-to-volume ratio) they must be considered likely sources of both urea and ammonia nitrogen (2a).

Our conception of the role of bacteria in marine plankton communities has also undergone a change in recent years. Bacteria are no longer considered to be the primary agents of nutrient remineralization (8b) (Pomeroy, 1970; 1975; Johannes, 1968) and may in fact compete directly with the phytoplankton for available nitrogen and phosphorus (8a). Thayer (1974) suggests that this latter possibility is especially likely in estuarine environments where one of the principle sources of fixed carbon for bacteria is *Spartina sp.* detritus (10) which is relatively deficient in both nitrogen and phosphorus. Thus for complete degredation of this carbon source, the bacteria need an alternate, compensatory supply of nitrogen such as nitrate, ammonia or urea.

Recent investigations also indicate that bacteria quickly and efficiently assimilate the more labile components of the dissolved organic carbon (DOC) pool (7) (Williams, 1970). It has even been suggested that the relatively low concentrations of small organic molecules in natural waters is a result of their rapid assimilation by the bacteria. The bulk of the DOC in natural waters is most likely the result of phytoplankton excretion (6a, 6b) (Anderson and Zeutschel, 1970; Thomas, 1971; Wright, 1975) with a lesser amount derived from excretion by herbivores and higher trophic level animals (5a, 4) (Webb and Johannes, 1967; Corner and Davies, 1971). On the basis of

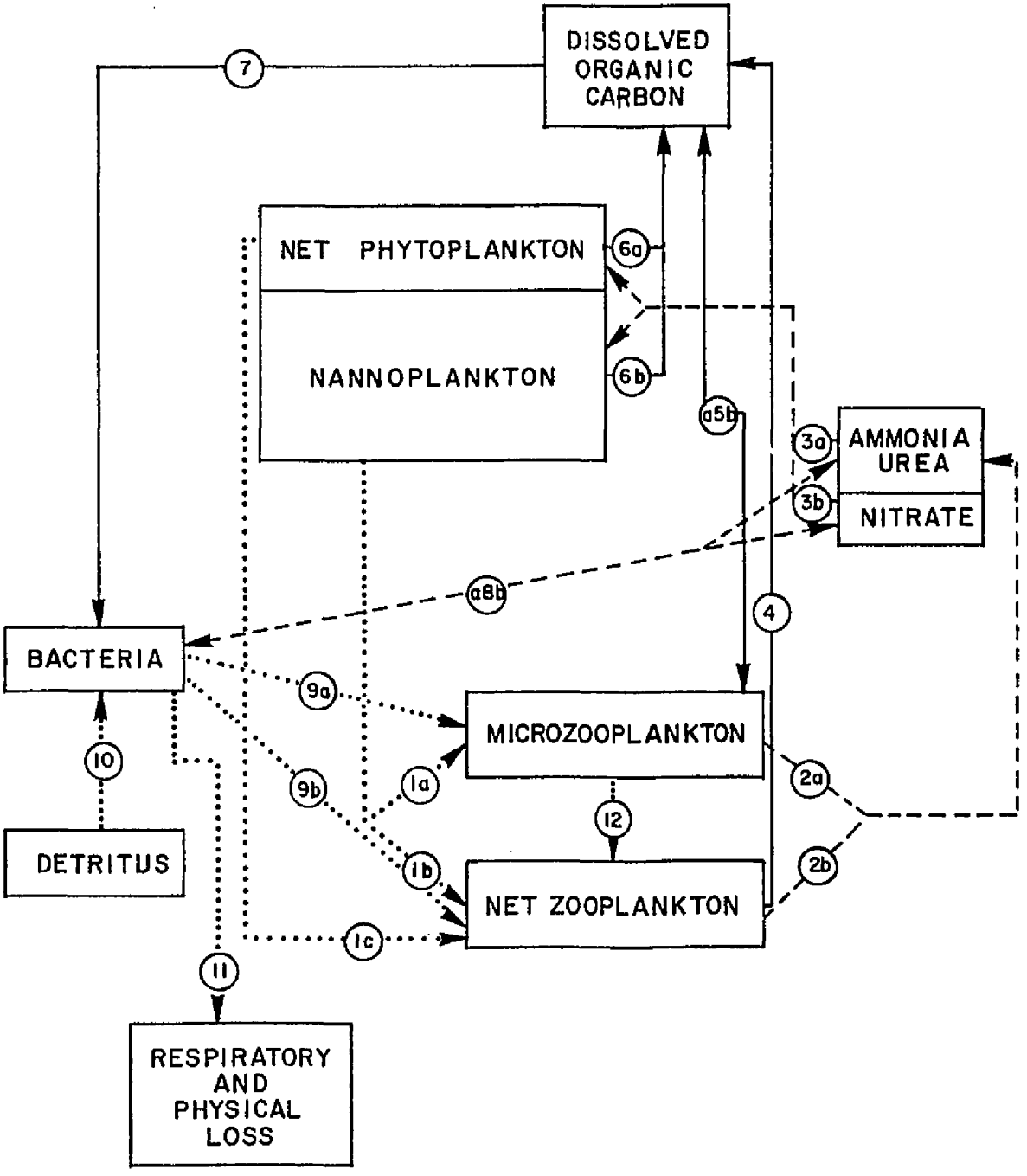
both their smaller storage capacity and their greater surface area-to-volume ratio, the nannoplankton may be expected to lose a higher proportion of their fixed carbon as DOC than the net plankton (6b). Based on measured rates of in situ bacterial utilization of DOC in the English Channel, the flow of carbon through this pathway was estimated to be 50% of the total carbon fixed by the phytoplankton (Andrews and Williams, 1971).

On the basis of their efficient utilization of DOC and their possible competition with the phytoplankton for nitrogen and phosphorus, the bacteria are potentially a significant component of the plankton food web. Their primary function is the return of DOC to the particulate food chain, although obligately heterotrophic protozoans such as ciliates and flagellates etc. may compete with the bacteria for DOC (5b). The liklihood of significant uptake of DOC by plankton bacteria is presumably enhanced in estuarine ecosystems where there is a close physical relationship between the euphotic zone and the sediments where bacterial numbers are likely to be highest. The extent to which bacteria are preyed upon by other components of the food web, thus completing the reentry of bacterial carbon, nitrogen and phosphorus back into the food web, is not presently clear (9a, 9b). Unless some pathway is functioning to effect this transfer, bacteria could conceivably act as a significant sink for removing these compounds from the plankton ecosystem, either through respiration or physical loss from the system (11).

The purpose of this study was to investigate the dynamics of the lower trophic levels of the lower York River, a temperate estuarine plankton community. Specifically the objectives were to: 1. elucidate

the dominant size component (in terms of energy flow) of the phytoplankton community; 2. To investigate the interactions between the abiotic and biotic components of these trophic levels by observing short term (i.e. hourly) changes in measured rate functions and concentration parameters associated with the plankton community; 3. To define the environmental factors that are functioning to regulate the metabolic activity and abundance of the phytoplankton community in this ecosystem; 4. To test the hypothesis, using laboratory cultures, that non-pigmented (i.e. obligately heterotrophic) nannoplankton are an alternative pathway (compared to bacteria) for the return of DOC to the particulate food web (5b); 5. To elucidate the factors regulating the physical hydrography of this estuarine system and delineate its effect on the dynamics of the plankton community.

Figure 1. Compartmental model of primary pathways of carbon (———), nitrogen (- - - -) and carbon and nitrogen (· · · ·) flux through the lower trophic levels of a temperate estuarine plankton ecosystem.


DISSOLVED ORGANIC CARBON
7
NET PHYTOPLANKTON
6a
NANNOPLANKTON
6b
a5b
3a
AMMONIA UREA
3b
NITRATE
a8b
4
BACTERIA
9a
MICROZOOPLANKTON
10
9b
1a
2a
12
DETRITUS
1b
2b
NET ZOOPLANKTON
1c
11
RESPIRATORY AND PHYSICAL LOSS

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THE EFFECT OF THE SPRING-NEAP TIDAL CYCLE ON THE VERTICAL SALINITY STRUCTURE OF THE JAMES, YORK AND RAPPAHANNOCK RIVERS, VIRGINIA, U. S. A.

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ABSTRACT

Analysis of salinity data from the lower York and Rappahannock Rivers (Virginia, U.S.A.) for 1974 revealed that both of these estuaries oscillated between conditions of considerable vertical salinity stratification and homogeneity on a cycle that was closely correlated with the spring-neap tidal cycle, i.e. homogeneity was most highly developed about 4 days after sufficiently high spring tides while stratification was most highly developed during the intervening period. The stratification-mixing cycle was generally more closely correlated with the height of high tide than with the magnitude of the tidal range. As a result of the annual cycle in the magnitude of spring high tides, periods of homogeneity were both more numerous and more intense in the late summer than in the winter. Variation in river flow appeared to be of secondary importance in regulating the hydrography of this estuary.

Analysis of salinity data collected during the period following Tropical Storm Agnes (July-August 1972) revealed that cycles of stratification and mixing occurred simultaneously throughout the entire salt influenced lengths of the James, York and Rappahannock Rivers. These cycles were similar to those described above and appeared to be a manifestation of the normal oscillatory nature of the estuaries and not a result of storm related flood waters.

INTRODUCTION

Estuaries are characterized primarily by their geomorphology and their pattern of salinity stratification (Hansen and Rattray, 1966). In coastal plain estuaries, the pattern of vertical salinity distribution is believed to be regulated primarily by the volume of freshwater flow and the magnitude of the tidal current. Thus, depending upon the relative magnitude of these two parameters, estuaries may be highly stratified (freshwater flow dominates tidal current), moderately stratified (freshwater flow and tidal currents relatively balanced), or vertically homogeneous (tidal currents dominate freshwater flow) (Bowden, 1967; Pritchard, 1967). Despite the acknowledged contribution, in theory at least, of tidal currents to the regulation of vertical salinity structure, most studies of estuarine hydrography have emphasized the effect of a variable freshwater flow (see examples in Dyer, 1973).

Salinity data collected in the lower York River during 1974 could be interpreted most easily by considering as an alternative a tidally-related control of the vertical salinity structure. This paper describes the relationship between the variation in the vertical salinity structure in the lower York and Rappahannock Rivers during 1974 and the cyclic variation in two tidal parameters. A similar relationship in the James, York and Rappahannock Rivers is described for a two month period in 1972.

METHODS AND MATERIALS

Description of the study area

The Chesapeake Bay and its subestuaries comprise the largest estuarine system in United States and have been classified by Pritchard (1967) as moderately stratified. The major tributaries of the lower Chesapeake Bay are the James, York and Rappahannock Rivers (Figure 1) and together they account for approximately 20% of the freshwater entering the Bay. The remainder is contributed primarily by the Potomac and Susquehanna Rivers, with the Susquehanna normally accounting for about 50% of the total input. Tides in the lower Chesapeake Bay are semidiurnal.

The James River is tidal for a distance of 170 kilometers (km) from its mouth and the 1.0 o/oo isohaline is normally located 55-95 km upriver. The mean tide range and surface salinities at the mouth are 0.8 meters (m) and 15-25 o/oo, respectively. With respect to hydrography, the James is the most thoroughly studied of the three rivers (for review see Pritchard, 1967).

The York River is formed by the confluence of the Pamunkey and Mattaponi Rivers about 50 km from its point of entry into the Chesapeake Bay. It is tidal throughout its entire length and the 1.0 o/oo isohaline is normally found 65-90 km from the mouth. The mean tidal range at the mouth is 0.7 m and the surface salinities at this point range from 15-24 o/oo. The lower York River is delimited at its upstream end by a constriction at Gloucester Point (Figure 2).

The Rappahannock River is tidal to the fall line at Fredricksburg, Virginia, a distance of 130 km from its mouth, and the 1.0 o/oo isohaline is normally found 75-90 km upriver. The mean tidal range and surface salinities at the mouth are 0.4 m and 12-18 o/oo, respectively. Longitudinal sections of the lower segments of each river are included in Figures 6, 7 and 8.

Data collection

Salinity data for the lower York River for 1974 were obtained from three sources: (1) monthly slack water runs by the Department of Physical Oceanography at the Virginia Institute of Marine Science (VIMS) in which salinity measurements were made at two meter depth intervals at three stations (Y0.0, Y6.7, Y8.9) in the lower York; (2) a dissolved oxygen study in the lower York River (Jordan, 1974) in which salinity was measured at two meter depth intervals biweekly at four stations (I, II, IV, V) and weekly at a fifth station (III); (3) a station at the York River mouth (B) that was occupied for eight different 24-48 hour periods in 1974 during which salinity was measured at two meter depth intervals every two hours. Station locations are shown in Figure 2. Data from a total of 195 hydrocasts representing 45 different days were analyzed.

Salinity data for the lower Rappahannock River were obtained from a study (Parker and Fang, 1975) that utilized surface and bottom salinometers at two stations, Norris Bridge and Smoky Point (Figure 1). Salinities were recorded half hourly from 18 June through 9 September at Norris Bridge and from 19 July through 9 September at Smoky Point.

During the two month period following Tropical Storm Agnes (July and August 1972) slack water runs were made by VIMS personnel in the James, York and Rappahannock Rivers on an approximately daily basis during the first month and approximately twice-weekly thereafter. Salinity was measured at two meter depth intervals at selected stations in each of the rivers (Figures 6, 7 and 8). The distribution of isohalines along the longitudinal section of the rivers was plotted for each sampling date (Hyer and Ruzecki, 1974).

River discharge to the lower York River was calculated by summing the mean daily flow rates (United States Department of the Interior, 1975) measured at gauging stations on the Pamunkey and Mattaponi Rivers (Figure 1), and multiplying by 1.54 to correct for the proportion of drainage area in the York River watershed below the gauging stations (Seitz, 1971). River discharge to the lower Rappahannock River was calculated by multiplying the mean daily flow rates measured at the Fredricksburg, Virginia gauging station (United States Department of the Interior, 1975) by a watershed correction factor of 1.39 (Seitz, 1971).

For this study, the surface-to-bottom salinity difference (Δ) was used as a relative measure of stratification, i.e. larger values of Δ indicate a greater degree of stratification. When more than one value of Δ was available from a single station for the same day, the mean was used and the number of observations indicated.

The mean daily tide range (R) and the mean daily high tide height (H) were both used as relative measures of the tidal current. Assuming all other conditions constant, the volume of water moving through a section of the estuary during a tidal cycle and hence the

tidal current is proportional to both the tide range and the stand of high water for that period. Values of R and H were computed from published tide tables (United States Department of Commerce, 1973) and represent predicted conditions at km 0-11 and km 15-40 in the York and Rappahannock Rivers, respectively. Values of R and H computed for the post-Agnes period (United States Department of Commerce, 1971) reflect conditions at Hampton Roads, Virginia with no correction for the individual river systems.

RESULTS

Results from two of the 24-48 hour stations reflect the wide range of stratification conditions observed in the lower York River during 1974. The mean value of Δ for 18-19 June was 8.6 o/oo (n=18) and the vertical distribution of salinity indicated a well stratified water column. The surface and bottom salinities for 21-22 August were all within the range of 20.4 o/oo to 20.7 o/oo and the mean value of Δ was 0.06 o/oo (n=14), indicating a vertically homogeneous water column.

Plotting the surface and bottom salinities from the lower York River against time revealed that the normally stratified water column was interrupted by periods of homogeneity, defined here as $\Delta \leq$ 1.0 o/oo, persisting up to four days (surface and bottom salinities from mid-June through August for stations Y0.0, I, III and B are shown in Figure 3). During 1974, homogeneity was observed in the lower York River on twelve occasions: 11 February; 28 March; 10 May; 4 and 26 June; 22-25 July; 9 and 21-23 August; 3 September; 7 October; 7 and 13 November (Figure 4).

Plotting the mean daily surface and bottom salinities from the Rappahannock River against time revealed that both stations underwent nearly identical monthly cycles of stratification and homogeneity (Figure 3). Comparison with the lower York River indicates that the three periods of homogeneity observed in the lower Rappahannock River (25-30 June; 19-29 July; 18-25 August) coincide with the periods of

homogeneity observed in the lower York River (shaded area Figure 3). However, the duration of homogeneity appears longer (8-10 days duration) and the magnitude of stratification less in the Rappahannock River than in the York River.

When plotted against time, the values of R and H describe both a lunar and annual periodicity (Figure 4). Two spring and neap tides per month are clearly expressed and in most instances there is marked inequality in the magnitude of adjacent spring tides and adjacent neap tides. The annual cycle of H is characterized by highest spring high tides from July through October and lowest spring high tides in December and February. The annual cycle of R shows maximal values in January-March and July-September and minimal values in April-May and November-December. The magnitude of both R and H is approximately two times greater in the lower York than in the lower Rappahannock (Figure 3).

Comparing the degree of stratification with the tidal cycle for the lower York River indicated that all eleven periods of homogeneity occurred one to six days following a spring high tide peak (Figure 4). Mixing appeared most intense following higher spring peaks (22-25 July and 21-23 August) while stratification appeared most highly developed following neap tide periods (Figure 3). On four occasions, 29 May; 10 June; 10 July; and 5 December, sampling during the six day period following a spring high tide peak did not reveal vertical homogeneity (Figure 4). The observation of homogeneity on 11 February, three days following a spring tide peak, was confined to four hydrocasts at Station B that measured values of Δ from 0.50 o/oo to 0.80 o/oo. However, the mean values of Δ for 11 and 12 February were 1.75 o/oo (n=9) and 5.25 o/oo (n=4), respectively.

Comparing the degree of stratification with the tidal cycles at the Rappahannock River stations indicated that maximum homogeneity occurred one to six days following the higher monthly spring tide peaks (shaded area Figure 3), resulting in a regular monthly pattern of stratification and homogeneity.

The apparent association between the spring-neap tidal cycle and the stratification-homogeneity cycle is illustrated by the linear regressions between log Δ and R or H (Table I). Combining all of the data from the lower York River, the highest correlation between Δ and either R or H was observed when a delay factor of -4 days was included in the tidal parameter i.e. salinity observation was correlated with the value of the tidal parameter observed four days previously. The goodness of fit for any given value of the delay factor from zero through -7 was always higher for Δ versus H than for Δ versus R. Restricting the regression to data collected at the three stations nearest the river mouth (Station B, I and Y0.0) further increased the goodness of fit (Table I).

For both Rappahannock River stations, the best fit between Δ and either R or H was also observed with a delay factor of -4 days. For the Norris Bridge data, the goodness of fit for any given value of the delay factor was higher for Δ versus H than for Δ versus R, while the reverse was true for the Smoky Point data (Table I). The better fit for Δ versus R at Smoky Point may be a result of the relatively short time span encompassed by the data. This is supported by the observation that limiting the Norris Bridge regression to data corresponding to the time span of the Smoky Point data greatly increased the best fit correlation of Δ versus R relative to Δ versus H for the

former station. All of the regressions in Table 1 indicate a very highly significant ($P<<0.001$) negative correlation between Δ and R or H.

The annual cycle of fluvial discharge into the lower York River for 1974 (Figure 5) indicated that lowest discharge occurred during July, August and October (monthly means < 30 m^3s^{-1}) while highest discharge occurred in January, March and April (monthly means > 100 m^3s^{-1}). The annual cycle of discharge calculated for the Rappahannock River was nearly identical in magnitude and periodicity to that of the York River.

During the post-Agnes period the James, York and Rappahannock Rivers exhibited similar cycles characterized by four alternating periods of stratification and homogeneity. The daily distribution of isohalines representing the most highly developed conditions of stratification and homogeneity observed in these rivers are shown in Figures 6, 7 and 8. The cycle of R and H for this time period was characterized by four consecutive, nearly equal and relatively large spring tide peaks (Figure 9).

A comparison of the tidal and stratification cycles revealed that in each river maximum observed stratification (2-4 and 18-21 July and 3-4 and 14-21 August) coincided with neap tides while maximum observed homogeneity (11-13 July, 31 July-1 August, 7-11 and 25-29 August) coincided with spring tides (Figure 9). Homogeneity was not observed in any of the rivers during the spring tide of 25-30 June. The two least developed periods of homogeneity (31 July-1 August and 8-11 August), typified by stratification persisting at the River mouths, coincided with the two lowest spring peaks. The period of the least developed stratification (3-4 August) coincided with the least developed and shortest of the four neap tide periods.

DISCUSSION

The phenomenon of an estuary regularly oscillating between conditions of vertical stratification and homogeneity in conjunction with the monthly spring-neap tidal cycle has not, to my knowledge, been previously reported. Presumably the increased turbulent mixing associated with increased tidal currents during spring tides causes the shift from a stratified to a well-mixed water column. Conversely, decreased turbulent mixing during neap tides permits the reimposition of stratification, presumably through the influx of higher salinity bottom water.

The generally better correlation between Δ and tidal height rather than tidal range may reflect the particular geomorphology of these estuaries. In a straight-sided estuary the volume of the tidal prism and hence the magnitude of the tidal current would be directly proportional to the tidal range and the tidal height, the latter assuming a constant level of low tide. However, the James, York and Rappahannock estuaries are bordered by lowlying marshes which flood on sufficiently high (i.e. spring) high tides, resulting in a disproportionately large tidal prism and hence greater tidal currents. Lower than normal (spring) low tides do not have a comparable effect. Since the magnitude of the tidal range is a cumulative function of the height of successive high and low tides, it follows that the stratification-mixing cycle should be more closely correlated with the height of high

tide than with the magnitude of the tidal range. As an example, the limited occurrence of homogeneity observed on 11-12 February is predicted more accurately by the small spring high tide peak on 8 February than by the large spring tide range peak on the same day, the latter resulting from extreme low tides.

The minimum value of H theoretically necessary to attain $\Delta <$ 1.0 o/oo, calculated from the equations in Table I, is 0.78 m for the lower York River. This may explain the absence of mixing observed on 10 June, 10 July and 5 December, all dates within six days following a spring high tide less than 0.78 m. However, on four occasions mixing was observed following spring high tide peaks less than the predicted minimal value (28 March; 10 May; 4 June and 9 August), suggesting that during these periods factors such as river flow or wind direction and velocity may be influencing the mixing process. The number of spring high tide peaks per month exceeding this minimum value and the number of consecutive days that each peak exceeds this value (Figure 4) suggests that both the occurrence and severity of mixing should be greater in the late summer-early fall than in winter. The results from the lower York River generally conform to this pattern, although this may also reflect the greater frequency of sampling during the summer.

The relatively restricted time span of the Rappahannock River data precludes its use in predicting the occurrence of mixing in other months of the year. However, it is apparent that cycles of stratification and mixing can occur on both a monthly (Figure 3) and bimonthly (Figure 9) basis in the Rappahannock River.

The extreme distance between the York River mouth and the gauging stations on its upper tributaries (ca. 100 and 150 km for the Mattaponi and Pamunky, respectively) complicates a quantitative assessment of the effect of freshwater flow on the hydrography of the lower River. However, the annual cycle of York River flow for 1974 appears to compliment rather than oppose the proposed effect of the spring-neap tidal cycle on vertical salinity distribution. Low river flows in late summer-early fall, in conjunction with high spring high tides, should enhance both the occurrence and intensity of mixing. Low river flow may have contributed to the four non-predicted periods of mixing previously described. Conversely, high river flows in winter, in conjunction with low spring high tides should favor the maintenance of stratified conditions. Despite the apparently complimentary relationship between river flow and tidal cycle, river flow is of secondary importance in regulating the hydrographic characteristics of this estuary. This is indicated by the irregular nature of freshwater flow compared to the regularity of the spring-neap tidal cycle, the short term (i.e. biweekly) periodicity of the stratification-mixing cycle and its correlation with the spring-neap tidal cycle.

The similarity between the post-Agnes stratification-mixing cycles and those observed in 1974, suggest that the former cycles were not a consequence of post-Agnes flooding, as suggested by Hyer and Ruzecki (1974), but were a manifestation of the normal oscillatory nature of the subestuaries. The return of both river flows (Ruzecki, 1974) and tidal heights (Jacobson and Fang, 1974) to near normal levels by the first week in July, support this conclusion.

Analysis of the daily change in the distribution of isohalines in the James, York and Rappahannock Rivers during 1972 revealed that vertical homogeneity originated in the upper segments of the saline influenced sections of each river and progressed downstream. This may be explained by lower vertical salinity gradients, increased area of marshland, greater tidal ranges and smaller river volumes upriver, all of which will enhance the possibility of the mixing phenomenon. The apparent initiation of vertical mixing upriver suggests that the magnitude of the delay factor derived from the best fit linear regressions is a function of the longitudinal position in the river, increasing negatively as one moves toward the mouth. The absence of a consistent delay period when entire river systems are considered (Figure 9), and the presence of such a factor when analysis is limited to data from the lower river segments (Table I) support this conclusion.

The extent to which the lower Chesapeake Bay exhibits the stratification-mixing cycle is presently unknown. However, the observation that the waters of the lower Bay vary with time from stratified to well mixed (G. C. Grant, personal communication) and the results of the post-Agnes sampling in the lower Bay (Kuo, Ruzecki and Fang, 1974) both suggest the presence of such a cycle. If the lower Bay functions primarily as an extension of its subestuaries then one might expect a response similar to that observed in the rivers, but with an increased delay period. If the lower Bay functions largely independent of its subestuaries it may either reflect a cycle different than the rivers or no cycle at all.

Both the extreme range of observed stratification conditions and the short response time of the system to the forcing function presumably causing these changes emphasizes the highly dynamic nature of these estuaries. It is apparent that conventional classification schemes which consider estuaries as essentially unchanging entities (i.e. moderately stratified, well mixed), are of limited utility with respect to the James, York and Rappahannock Rivers. Hansen and Rattray's (1966) method of classification does reflect the capability of variable factors to alter the hydrographic patterns of an estuary, and appears to be more appropriate for the systems considered in this study. However, the primary regulating factor in these estuaries appears to be the biweekly variation in the tidal current rather than the annual variation in river flow.

Increased understanding of the hydrographic characteristics of these estuaries may contribute to increased understanding of other aspects of the total ecology of the system. Plankton production in coastal and oceanic areas has been shown to be influenced by the degree of stratification and mixing (Gran and Braarud, 1935; Sverdrup, 1953). The concentration and distribution of suspended sediments in estuarine systems is effected by the tidal currents (Postma, 1967). The apparent predictability of the stratification-mixing process is of particular value. Results of biological studies can be interpreted with a better knowledge of the past history of the biota. The results of past studies can be reinterpreted in the light of these new findings. Future studies can be planned to take into account the widely varying hydrographic conditions that might be expected.

Regardless of the eventual ramifications of these findings with respect to our perception of the lower Chesapeake Bay and its subestuaries, it is apparent that a regulatory factor which heretofore has been largely overlooked in studies of estuarine hydrography, is playing a significant role. It is imperative therefore, that subsequent studies are properly designed to elucidate the possible contribution of a variable tidal parameter to estuarine hydrography and ecology.

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Figure 1. Lower Chesapeake Bay with the James, York and Rappahannock Rivers. Sampling stations in the Rappahannock River and gauging stations on the Mattaponi and Pamunkey Rivers are shown.

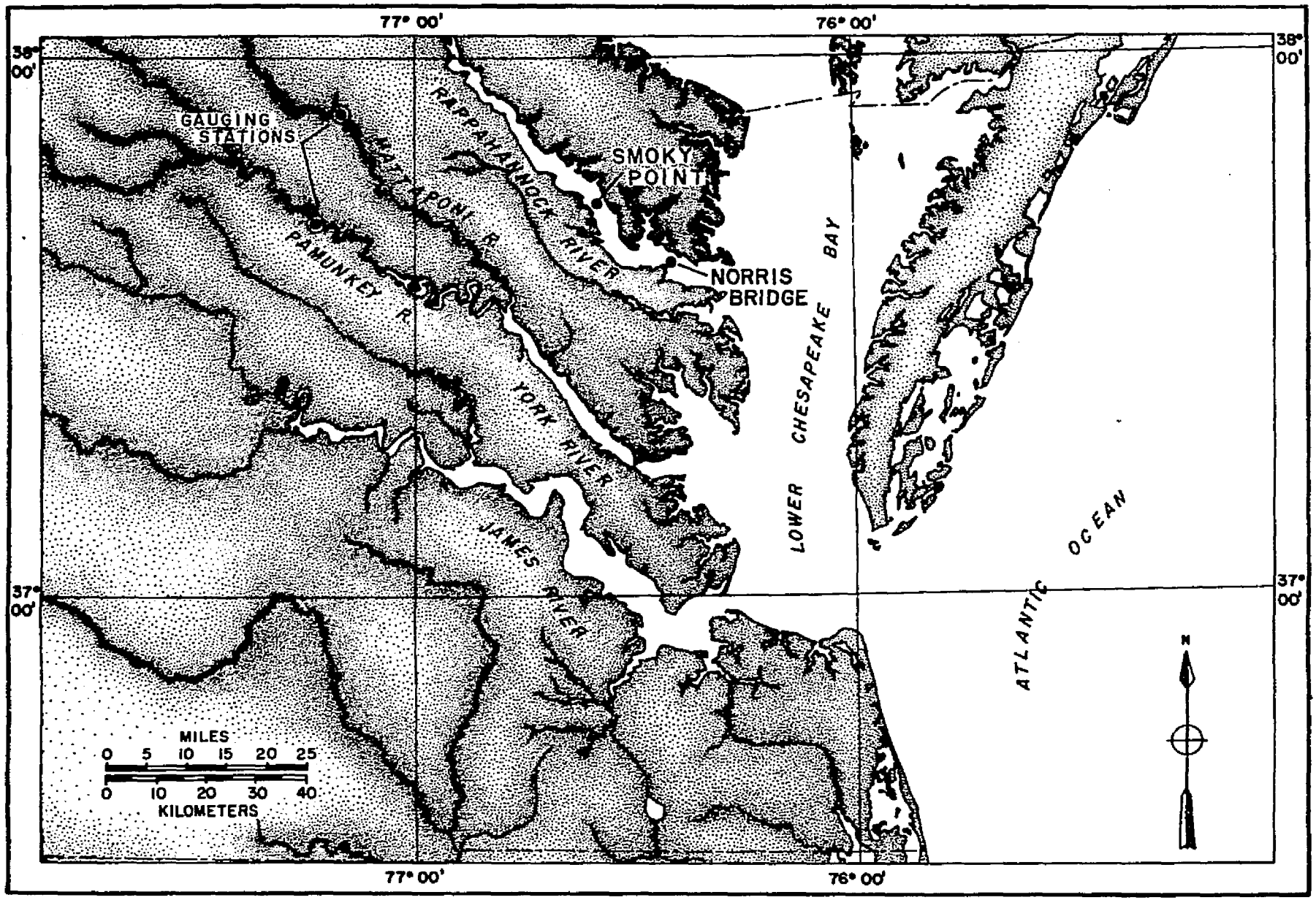
77° 00'
76° 00'
38° 00'
37° 00'
GAUGING STATIONS
MATTAPONI R.
PAMUNKEY R.
RAPPAHANNOCK RIVER
SMOKY POINT
NORRIS BRIDGE
YORK RIVER
JAMES RIVER
LOWER CHESAPEAKE BAY
ATLANTIC OCEAN
MILES
0 5 10 15 20 25
0 10 20 30 40
KILOMETERS
N

Figure 2. Lower York River showing location of sampling stations. 5.5 meter depth contour is shown.

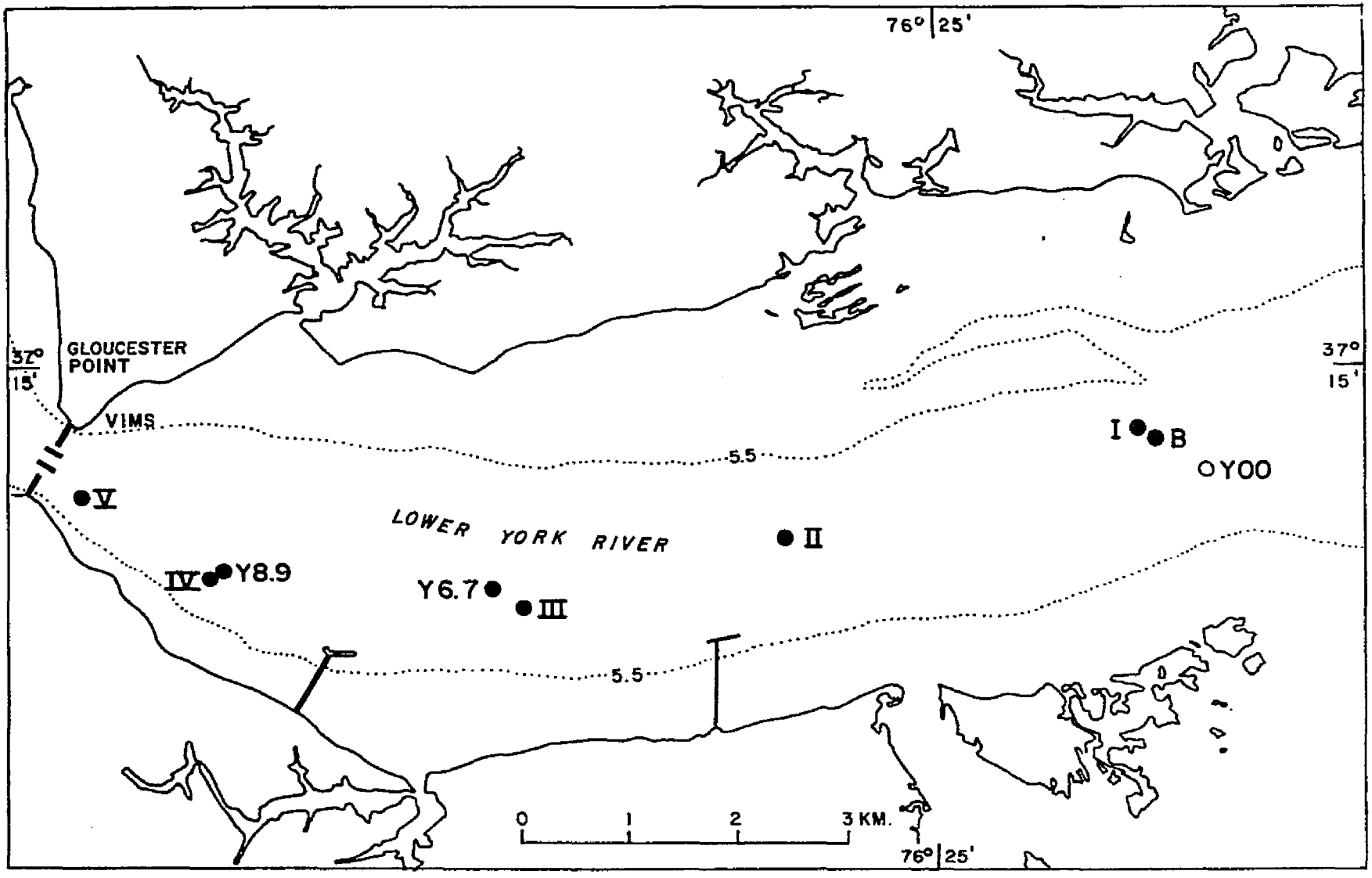
76° 25'
37° 15'
GLOUCESTER POINT
VIMS
5.5
I
B
Y00
V
LOWER YORK RIVER
II
IV
Y8.9
Y6.7
III
5.5
0 1 2 3 KM.
76° 25'
37° 15'

Figure 3. Values of predicted tidal range (R), predicted high tide height (H), and surface (- - -) and bottom (——) salinities for the lower York River (left hand axis) and lower Rappahannock River (right hand axis) during the period 10 June through 31 August 1974. Shaded areas illustrate the relationship between periods of maximum values of R and H and periods of homogeneity in the lower York and Rappahannock Rivers.

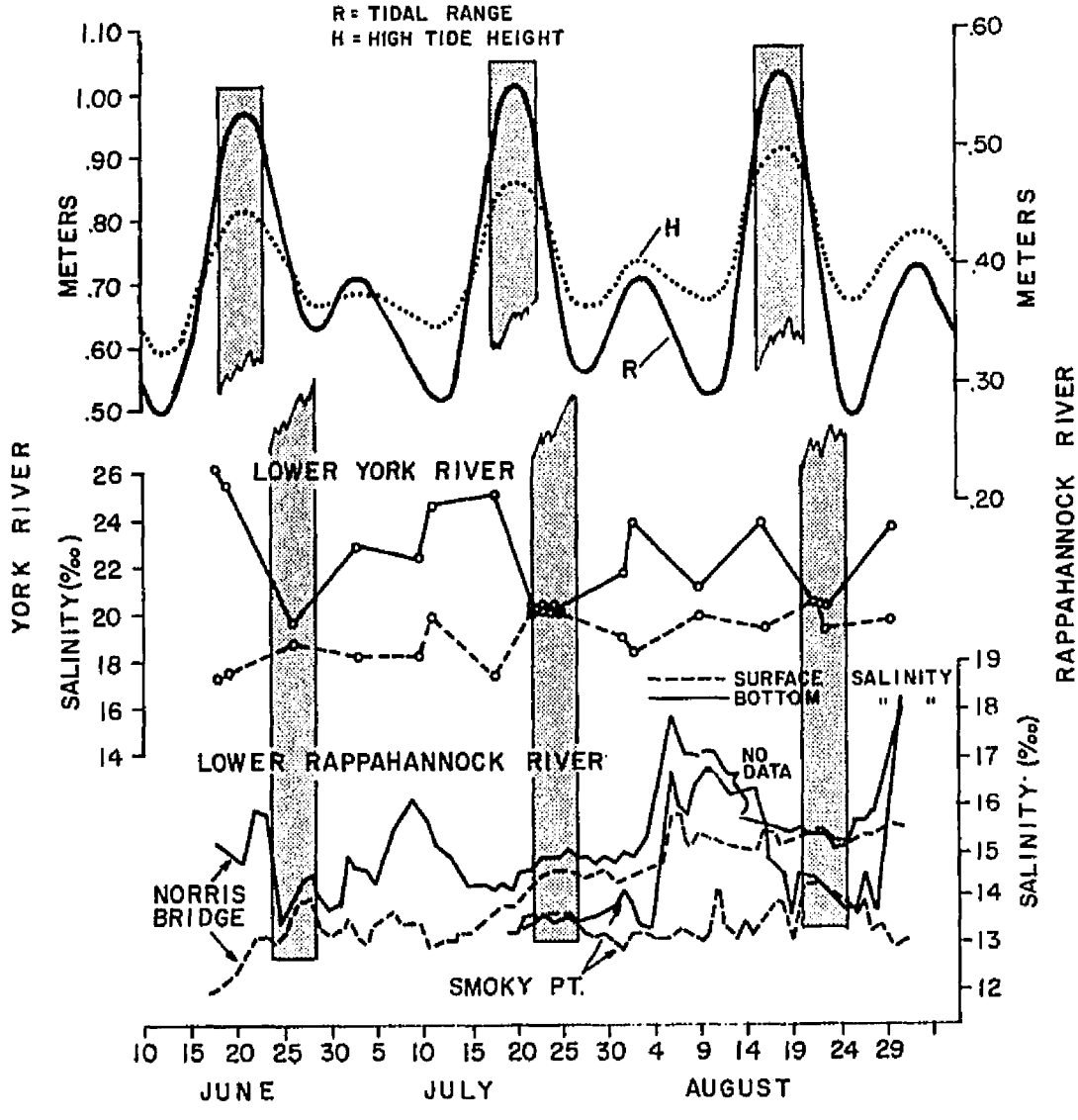
R = TIDAL RANGE
H = HIGH TIDE HEIGHT
METERS
1.10
1.00
.90
.80
.70
.60
.50
H
R
.60
.50
.40
.30
.20
METERS
YORK RIVER
RAPPAHANNOCK RIVER
LOWER YORK RIVER
SALINITY(‰)
26
24
22
20
18
16
14
SURFACE SALINITY
BOTTOM " "
LOWER RAPPAHANNOCK RIVER
NO DATA
NORRIS BRIDGE
SMOKY PT.
19
18
17
16
15
14
13
12
SALINITY (‰)
10 15 20 25 30 5 10 15 20 25 30 4 9 14 19 24 29
JUNE
JULY
AUGUST

Figure 4. Values of mean daily tidal range (——) and mean daily high tide height (····) for the lower York River for 1974. Days on which vertical salinity homogeneity were observed are indicated ●, vertical salinity stratification observations are indicated ■. Horizontal line indicates a tidal magnitude of 0.78 meters.

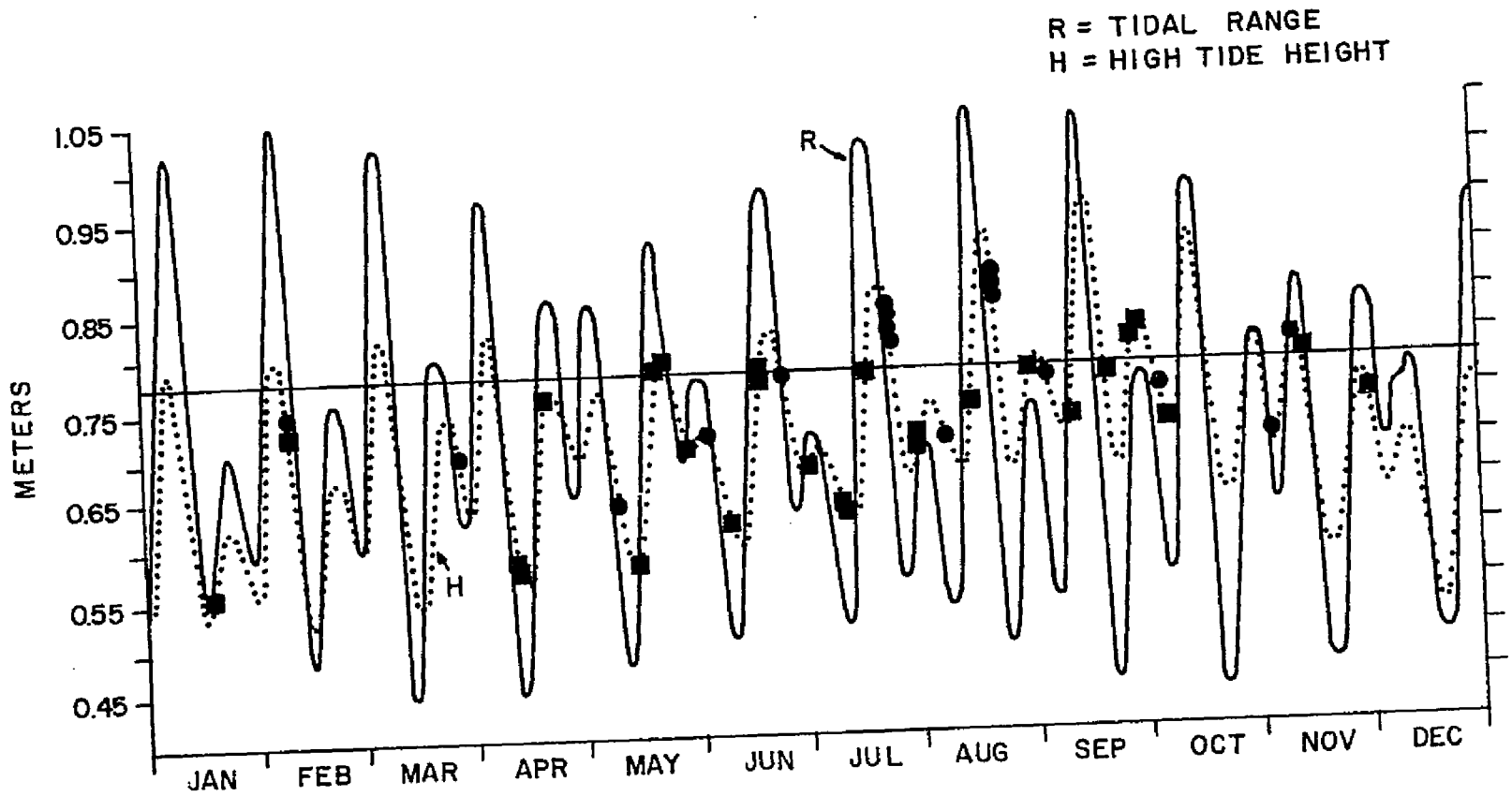
R = TIDAL RANGE
H = HIGH TIDE HEIGHT
METERS
1.05
0.95
0.85
0.75
0.65
0.55
0.45
R
H
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC

Figure 5. Mean daily rates of freshwater flow to the lower York River for 1974.

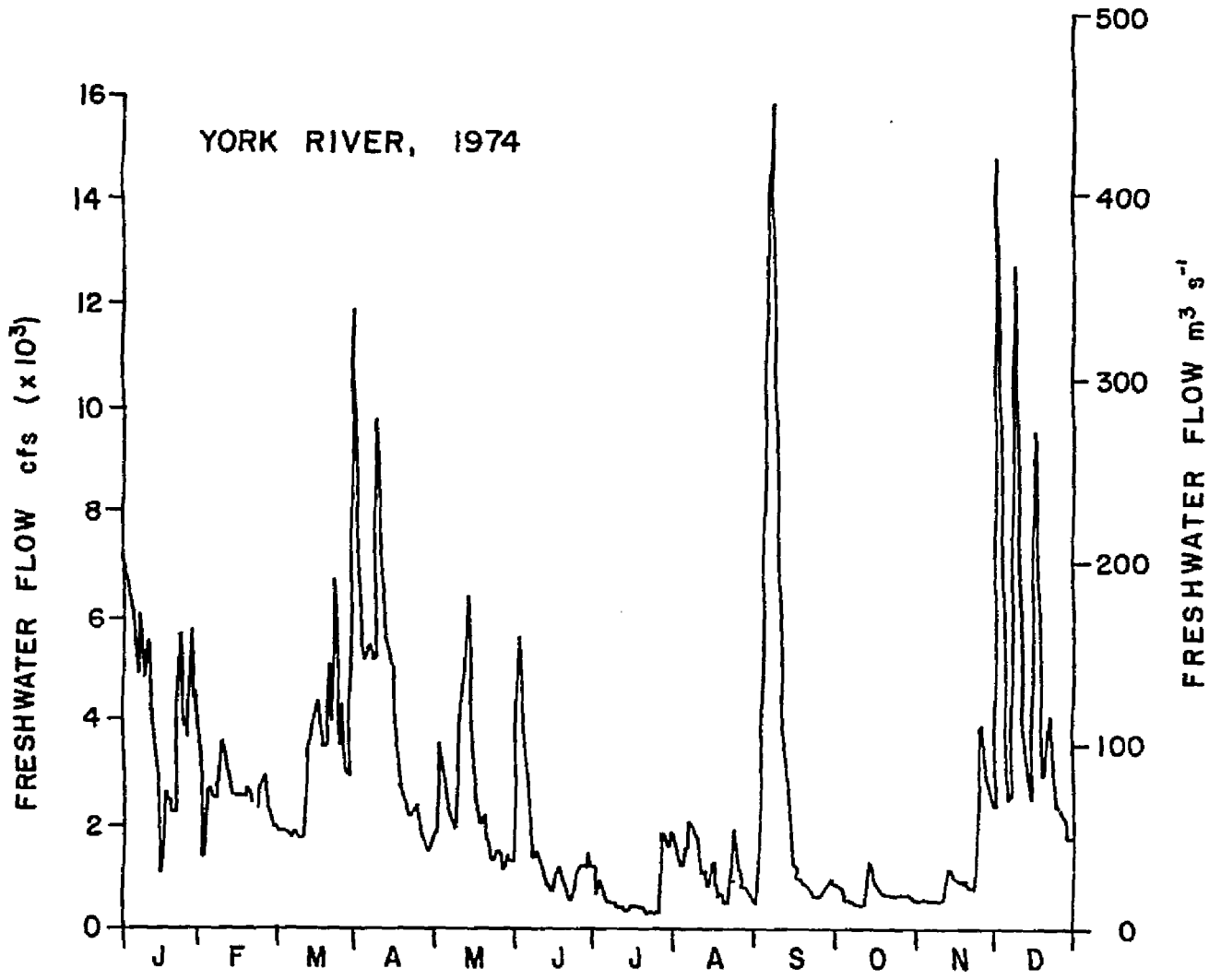
YORK RIVER, 1974
FRESHWATER FLOW cfs (x 10³)
FRESHWATER FLOW m³ s⁻¹
0
2
4
6
8
10
12
14
16
0
100
200
300
400
500
J
F
M
A
M
J
J
A
S
O
N
D

Figure 6. Distribution of isohalines on the longitudinal section of the James River for selected days during the post-Agnes period, illustrating alternating periods of maximum observed stratification (left hand column) and homogeneity (right hand column). (Taken from Hyer and Ruzecki, 1974).

JAMES RIVER

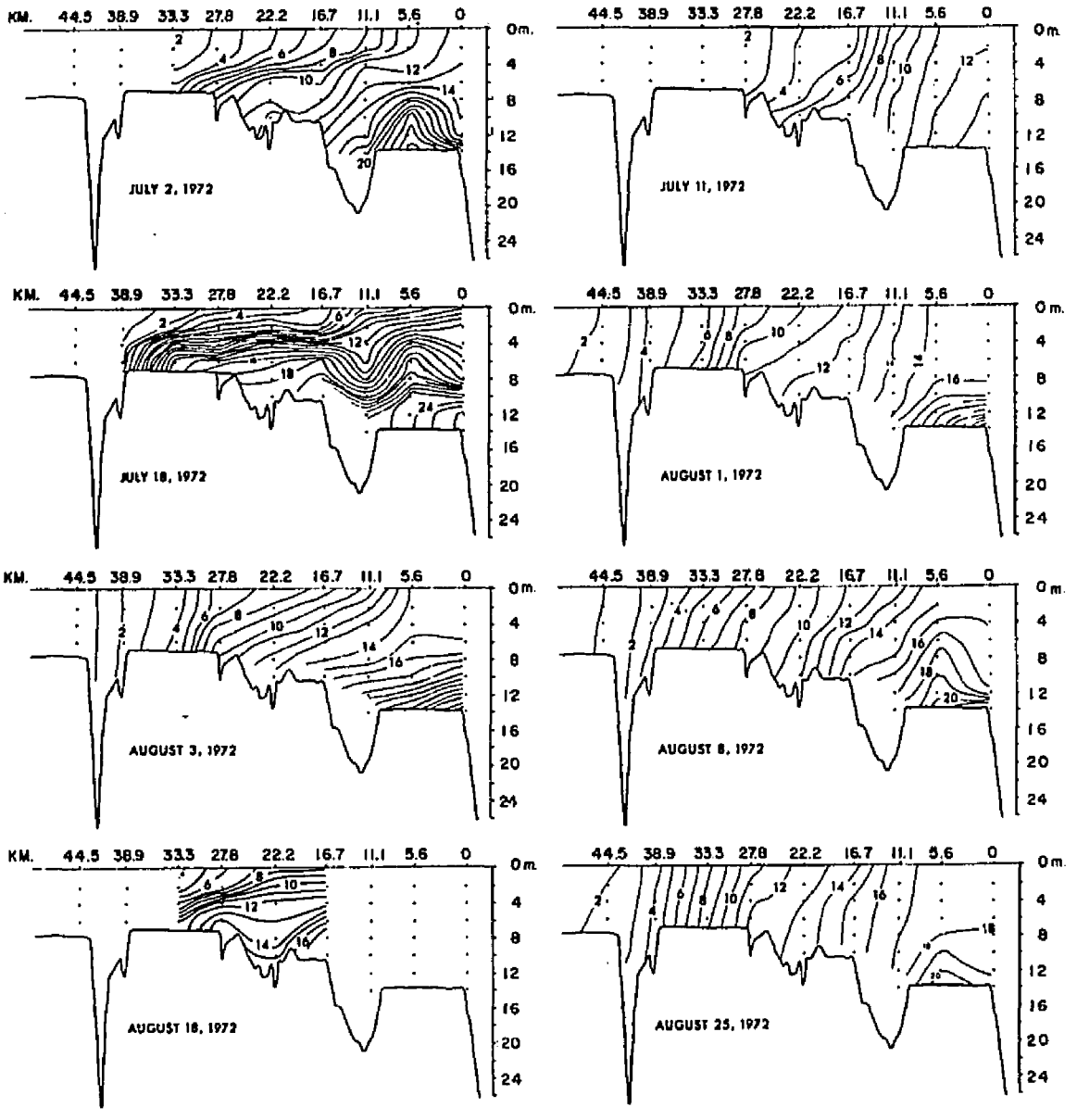
KM. 44.5 38.9 33.3 27.8 22.2 16.7 11.1 5.6 0
0m.
4
8
12
16
20
24
JULY 2, 1972
JULY 11, 1972
JULY 18, 1972
AUGUST 1, 1972
AUGUST 3, 1972
AUGUST 8, 1972
AUGUST 18, 1972
AUGUST 25, 1972

Figure 7. Distribution of isohalines on the longitudinal section of the York River for selected days during the post-Agnes period, illustrating alternating periods of maximum observed stratification (left hand column) and homogeneity (right hand column). (Taken from Hyer and Ruzecki, 1974).

YORK RIVER

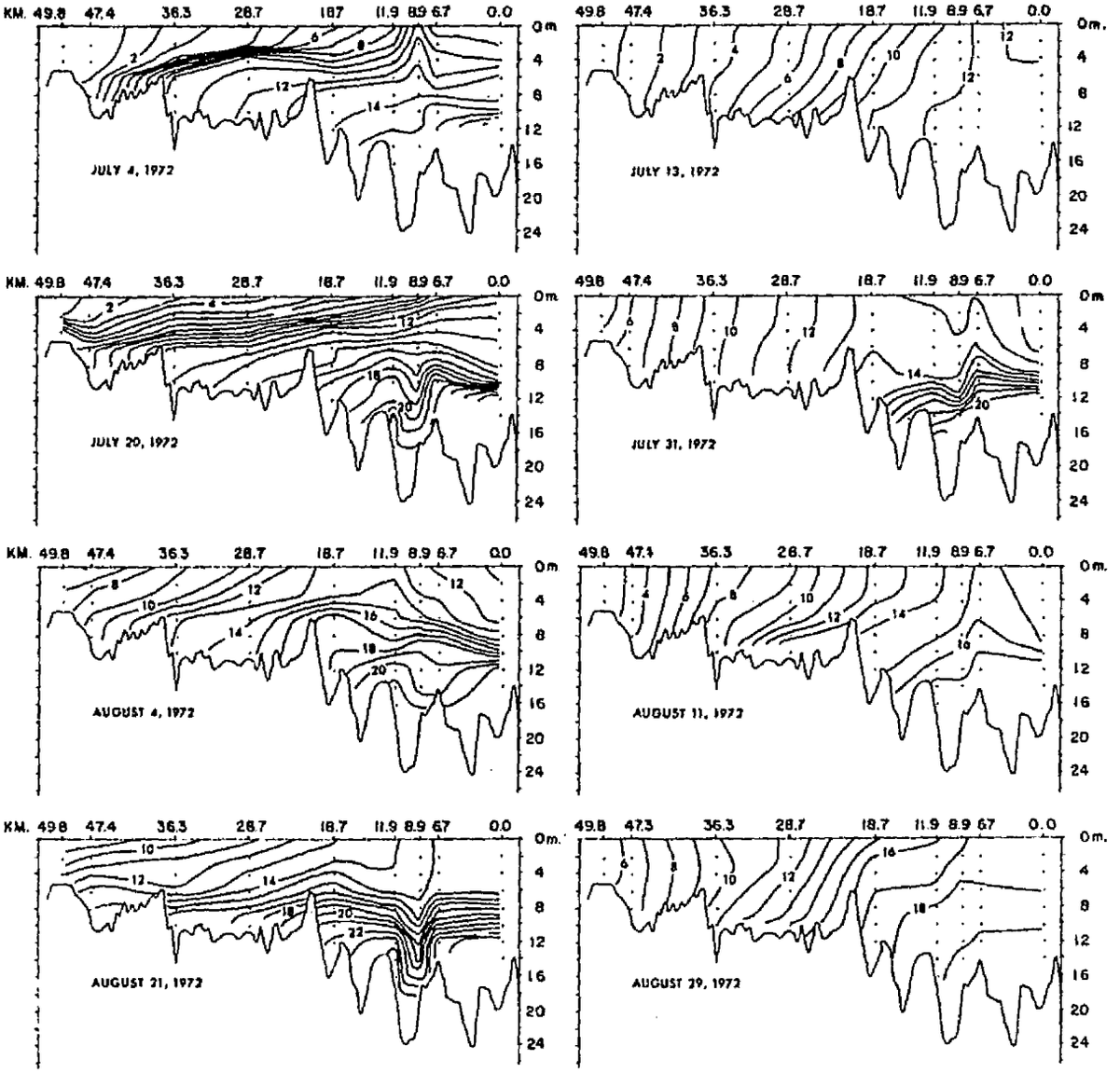
KM. 49.8 47.4 36.3 28.7 18.7 11.9 8.9 6.7 0.0
Om
4
8
12
16
20
24
JULY 4, 1972
JULY 13, 1972
JULY 20, 1972
JULY 31, 1972
AUGUST 4, 1972
AUGUST 11, 1972
AUGUST 21, 1972
AUGUST 29, 1972

Figure 8. Distribution of isohalines on the longitudinal section of the Rappahannock River for selected days during the post-Agnes period, illustrating alternating periods of maximum observed stratification (left hand column) and homogeneity (right hand column). (Taken from Hyer and Ruzecki, 1974).

RAPPAHANNOCK RIVER

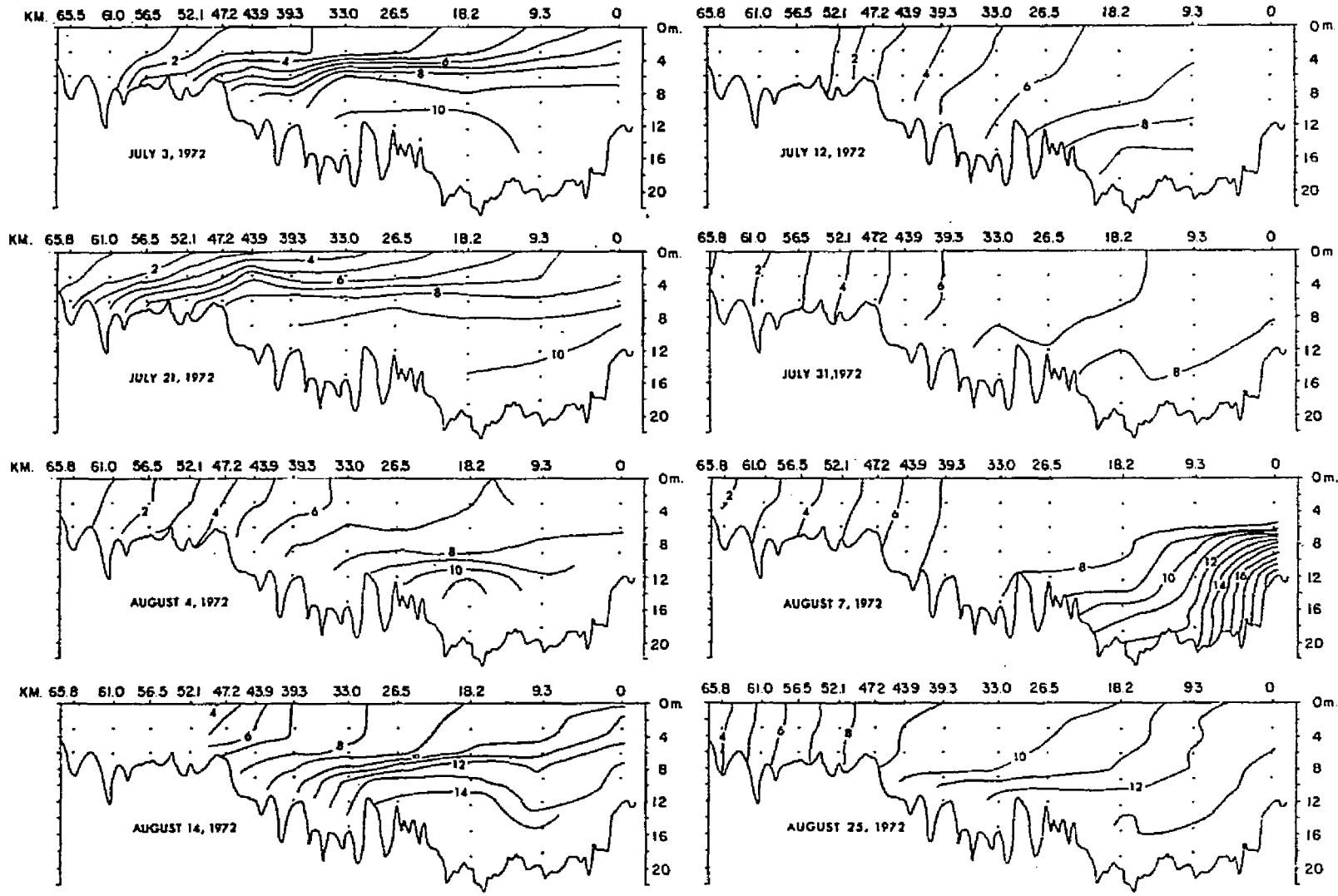

Figure 9. Values of predicted tidal range (———) and predicted high tide height (·····) for the period 20 June through 31 August, 1972 at Hampton Roads, Virginia. Periods of maximum observed homogeneity (◯) and maximum observed stratification (□) in the James (J), York (Y) and Rappahannock (R) Rivers are indicated.

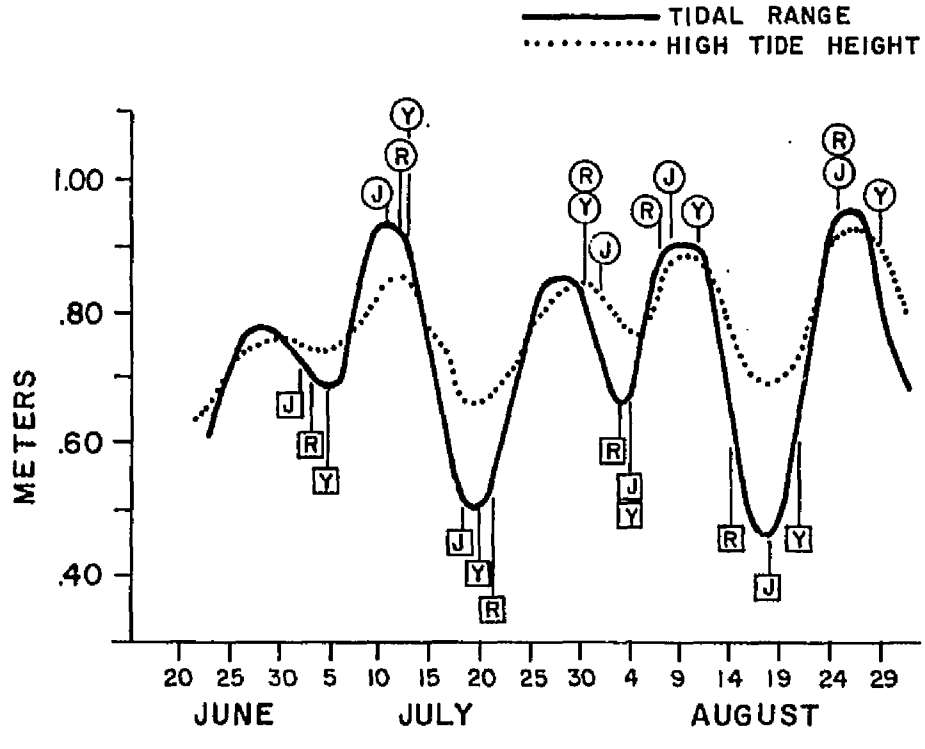
TIDAL RANGE
HIGH TIDE HEIGHT
METERS
1.00
.80
.60
.40
20 25 30 5 10 15 20 25 30 4 9 14 19 24 29
JUNE
JULY
AUGUST

TABLE I.

Best fit linear regressions for the logarithm of the surface-to-bottom salinity difference (log Δ) versus predicted tidal range (R) or predicted high tide height (H). Correlation coefficient (r), the value of t and the number of observations (n) are shown for each regression.

Stations	Regressions	r	t	n
YORK RIVER				
Lower York	$\log \Delta = -2.19\ R_{-4} + 1.83$	-0.584	7.62**	114
Lower York	$\log \Delta = -5.21\ H_{-4} + 4.03$	-0.669	9.51**	114
River Mouth	$\log \Delta = -6.42\ H_{-4} + 4.97$	-0.71	10.79**	39
RAPPAHANNOCK RIVER				
Norris Bridge	$\log \Delta = -9.43\ H_{-4} + 3.62$	-0.706	8.55**	76
Smoky Point	$\log \Delta = -8.74\ R_{-4} + 3.08$	-0.763	8.43**	53

**indicates very highly significant correlation ($P<<.001$)

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PHYTOPLANKTON DYNAMICS IN A TEMPERATE ESTUARY[1,2]

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running head: Phytoplankton dynamics in a temperate estuary

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ABSTRACT

A station in the lower York River (salinity 15-25 o/oo; depth ca. 18 meters) was occupied on eight separate occasions (24-36 hour duration) during 1974 for thepurpose of studying the phytoplankton dynamics in this temperate estuarine system. Chlorophyll a (Chl a) and ^{14}C in situ primary production (PP) for both the total phytoplankton and nannoplankton (< 15 μm) were measured at four depths in the euphotic zone at regular intervals. The nannoplankton accounted for 65-90% of the total Chl a and PP during each station except February (55% Chl a and 19% PP) and May (44% Chl a and 37% PP). Nannoplankton influence appeared to peak in late summer. Maximum daily Chl a levels ranged from 5-25 μg l^{-1} with no apparent seasonal trend. A diel variation was observed in Chl a abundance with highest concentrations at mid afternoon and lowest concentrations at midnight to 0300. The daily increase in nannoplankton Chl a generally doubled the minimum daily concentration. Plots of assimilation ratio (μgC hr^{-1}μg Chl a^{-1}) versus in situ light intensity for both the total and nannoplankton resembled typical photosynthesis versus light intensity curves (i.e. hyperbolic) with no inhibition observed at light levels up to 0.6 langleys min^{-1}. A diel variation was observed in assimilation ratios with highest values in the afternoon on short and medium length days and high morning and afternoon values separated by a noontime depression on long days. Light saturated assimilation ratios (Pmax) were generally

correlated with temperature. However, Pmax values in July and August were reduced to 50% of the June values (at comparable temperatures) presumably a result of shade adaptation associated with a surface mixed layer 5-6 times deeper than the euphotic zone. High Pmax values for the net plankton (> 15 μm) in February were presumed to be due to temporal succession of a cold adapted species. The results suggest that a highly dynamic nannoplankton community exists in this estuary, possibly doubling every 24 hours but with biomass accumulations limited by grazing. It is proposed that a close coupling exists between zooplankton grazing, ammonia excretion and phytoplankton ammonia assimilation and that seasonal production is influenced by hydrographic conditions which regulate the degree of stratification and mixing.

INTRODUCTION

Despite the high primary productivity that is characteristic of temperate estuarine systems, our knowledge of the dominant phytoplankton species and the factors regulating their production in these environments is still limited. One approach to increasing our understanding of the dynamics of these systems is to capitalize on the closely linked relationship between the organism and the environment that is characteristic of phytoplankton (Harris and Lott, 1973). In this manner, large and small scale changes (in time and space) in phytoplankton parameters can be related to environmental changes and a cause-effect relationship elucidated.

The effectiveness of this approach may be enhanced by considering relatively recent changes in our concept of phytoplankton dynamics. For example, past emphasis on nutrient limitation of phytoplankton production has obscured the fact that other factors such as temperature, light, grazing and hydrographic features, acting either singly or in combination, may regulate the phytoplankton. This is especially likely in temperate estuaries which are relatively nutrient rich compared to other marine environments.

In recent years, there has been an increasing awareness of the significant role of the very small phytoplankton (< 15 μm, i.e. the nannoplankton) in plankton communities (Pomeroy, 1974). When the present study was initiated, however, there was no quantitative

information on the contribution of nannoplankton to the primary production of the Chesapeake Bay despite previous evidence of their likely significance (Mackiernan, 1968; Marshall, 1967; Patten, Mulford and Warinner, 1963).

In the past, most phytoplankton studies emphasized seasonal variation in plankton parameters. However, a growing awareness of the propensity of phytoplankton to undergo diel variations (Sournia, 1974) is changing this experimental approach. Increased comprehension of diel cycles has both practical and heuristic implications for plankton research. In the former case, understanding diel periodicities is necessary to properly evaluate the results of single daily samples, a necessary constraint in many phytoplankton investigations. In the latter case, a better comprehension of diel cycles may help to elucidate interrelationships between organisms and the environment that cannot be perceived by discrete sampling over longer intervals i.e. days or weeks.

In 1974, a study of phytoplankton dynamics in the lower York River was undertaken with the following objectives: to determine the contribution of the nannoplankton to the total phytoplankton community; to elucidate the diurnal variability inherent in these communities; and to gain some insight into the factors regulating phytoplankton production in this environment.

STUDY AREA

The York River is typical of the coastal plain-drowned river vally estuaries that characterize the major tributaries of the Chesapeake Bay and the Bay itself. The lower York River, in which this study took place, has an average width of 2.5 km. and an average depth of 8.5 m (Fig. 1). A channel 16-18 m. in depth extends the entire length of the lower river and continues to the mouth of the Chesapeake Bay. The annual range of surface temperatures and salinities are typically 2-28°C and 15-25 o/oo, respectively. The tides are semi-diurnal with a mean amplitude of 0.7 m. and a mean tidal excursion of about 7 km. Freshwater discharge is lower in the summer and early fall and highest in the winter and early spring.

The unique hydrographic characteristics of this estuarine system have been described (Haas, 1975) and are briefly summarized here. The major tributaries of the lower Chesapeake Bay (the James, York and Rappahannock Rivers) regularly oscillate between conditions of vertical stratification and homogeneity on a cycle that is closely correlated respectively with the neap and spring tides. In the lower York River periods of vertical mixing lasting from 4-6 days are most highly developed four days after sufficiently high spring tides. As a result of higher spring tides and lower freshwater runoff during the summer and early fall, periods of vertical mixing are likely to be both more severe and more frequent (two per month) than in the winter when stratified conditions may exist throughout the month.

METHODS AND MATERIALS

During 1974 a station located mid-channel at the mouth of the York River (depth 18 m) was occupied for periods of 24-36 hours on eight different occasions: 11-12 February; 16-17 April; 21-22 May; 18-19 June; 23-24 July; 21-22 August; 1-2 October; and 13-14 November.

Samples for temperature, salinity and dissolved oxygen were collected with a submersible pump at two meter depth intervals every two hours for the duration of the station. Temperature was measured to the nearest 0.2°C with a thermistor (Yellow Springs Instrument Co.). Salinity was measured using a Beckman RS-7B Induction Salinometer. Dissolved oxygen was measured by Winkler titration following the procedures of Strickland and Parsons (1972). The percent oxygen saturation was calculated with a nomogram from Green and Carritt (1967). Extinction coefficients (k; m^{-1}) were calculated from periodic measurements of light penetration in the water column made with an underwater photometer equipped with a cosine filter (G. M. Mfg. Corp. Model 268WA310). A continuous measure of incident radiation was recorded on a pyroheliometer located 10 km. from the station. Light was measured in the units of cal cm^{-2} min^{-1} (langleys min^{-1} or ly min^{-1}). Consequently, the mean integrated light intensity for any time span could be calculated for any depth.

Phytoplankton production was measured by the ^{14}C technique (Steemann-Nielsen, 1952) on water collected from depths of 0.5, 1.0,

2.0 and 4.0 m every two hours during the first day (sunrise to sunset) of each station. Triplicate 20 ml. aliquots from each depth were placed in 30 ml. capacity screw cap vials (two light, one dark) to which 0.4 to 1.0 μCi of ^{14}C labeled sodium carbonate was added. The vials were returned to their respective sampling depths in the water for two hours, whereupon they were retrieved and the contents fixed with buffered formalin (final concentration 3%).

The contents of the vials were filtered onto Celotate^{R} (Millipore Corp.) filters (nominal pore size 0.5 μm) that had been prewetted with filtered seawater. After rinsing the vial and filter, once each, with 5.0 ml. of filtered seawater, the damp filters were placed in scintillation vials to which 0.2 ml of NCS^{R} (Amersham/Searle) was added and allowed to stand overnight. Ten milliliters of scintillation cocktail (4.0 g PPO and 50 mg POPOP per liter toluene) was added to each vial at least two hours prior to counting in a liquid scintillation counter (Beckman LS-150) with a ^{14}C counting efficiency of 90%. Total carbon dioxide content of the water (CO_2+H_2CO_3+HCO^-+CO_3^{2-}) was measured with a carbon analyzer (Beckman model 915). Rates of productivity were computed following Strickland and Parsons (1972).

Chlorophyll *a* was used as a measure of phytoplankton biomass and was measured by the fluorescence technique of Yentsch and Menzel (1963). Aliquots from each primary production sample as well as water samples from identical depths taken every two hours for the remainder of each station were analyzed. The water (100 ml) was filtered through a Gelman type A glass fiber filter which was immediately frozen. The pigment was extracted by homogenizing the filter in 90% acetone and allowing the sample to stand overnight in the dark. Pigment content

was measured with a Turner model 111 fluorometer.

The contribution of the nannoplankton to both total primary production and chlorophyll a was determined by gently filtering an aliquot of the original water sample through a 15 μm (Nitex^{R}) net before the appropriate analyses were performed. The contribution of the net plankton (i.e. those plankton retained by the 15 μm net) was determined by the difference between the filtered and unfiltered samples. The advantages of the prescreening method are discussed by McCarthy et al. (1974).

RESULTS

Near surface temperatures and surface and bottom salinities were averaged for the first day of each station (Table 1). Lowest temperatures were encountered in February, highest in July and August. The lowest surface salinities were observed in April, the highest in November.

The mean daily extinction coefficient and the corresponding 1% light level, considered to be the depth of the euphotic zone, are shown for each station (Table 1). The values suggest a seasonal trend with greatest light penetration in the winter and more turbid waters in the summer. The pyroheliometer readouts as well as total incident light (langleys day^{-1}) for the initial day of each station are shown in Figure 2. Except for the August station, moderate to full sunlight was encountered during all stations.

A comparison of surface-to-bottom salinity differences (values of Δ, Table 1) indicate that during the July and August stations, the entire water columns were well mixed. During the April, May, June and October stations the water columns were stratified. The trend of surface-to-bottom salinity differences during the February and November stations (increasing and decreasing, respectively) and the relative stage of the spring-neap tidal cycle during each station, indicate that the February water column was transitional from a mixed to a stratified condition while the November water column was transitional from a stratified to a mixed condition.

An alternative measure of the extent of vertical mixing is the depth of the surface mixed layer, calculated as the depth interval with the greatest change in salinity with respect to the total surface-to-bottom difference (Table 1). During the periods of intense vertical mixing (July and August), the depth of the mixed layer is equal to the total water depth. The most shallow mixed depth was observed in June. During the April station, an insufficient number of salinities from intermediate depths, precludes determination of the mixed layer depth. The ratio mixed layer depth:euphotic zone depth was calculated for each station (Table 1). Highest values (ca. 5-6) were observed in July and August and the lowest values (ca. 1.5) were observed in May and June.

Dissolved oxygen concentrations in the euphotic zone exhibited a persistent diel variation with maximum values normally observed in the late afternoon and minimal values observed prior to sunrise. The maximum and minimum daily levels were determined by averaging the 0.5, 1.0 and 2.0 meter values for three consecutive sampling periods (Table 1). Differences between the daily extremes generally increased with temperature. The low value for August probably resulted from the low level of incident radiation on that day. In summer, the concentration of dissolved oxygen in the euphotic zone was higher during periods of stratification than during periods of mixing. The low values during the periods of mixing resulted primarily from the mixing of oxygen depleted bottom water with surface waters.

Most of the observed chlorophyll values were within the 5-25 $\mu g\ l^{-1}$ range that is characteristic of the lower Chesapeake Bay (McCarthy and Taylor, 1974; Patten et al., 1963). In the absence of

any consistent variation in chlorophyll within the top four meters, the values were averaged for each sampling period and plotted against the time of day for each station (Fig. 3). Total chlorophyll was highest in October and lowest in November, and no distinct seasonal trend is evident. However, a consistent diel variation in chlorophyll abundance is evident. Concentrations increased in early morning and normally reached a peak in mid-afternoon, this was followed by a fairly rapid decrease with minimal concentrations observed from midnight to 0300. The diel variations were generally more pronounced for the nannoplankton than for the net plankton. However, in February the diel variation was observed only for the net plankton; the nannoplankton abundance remained relatively constant (Fig. 3). In May, there was no apparent diel variation in either size fraction (Fig. 3). The diel variation for the nannoplankton chlorophyll is shown in Figure 4. The mean bihourly values were expressed as a percent of the minimum daily mean, then averaged for all stations except February and May, and plotted against time of day. The results indicate that the daily nannoplankton chlorophyll increase tended to double the daily minimal concentration. In June, July and August, the variation in chlorophyll abundance was also related to the stage of the daily tidal cycle. However, this relationship was not consistent from month to month and in each instance was overshadowed by the diel cycle.

The contribution of the nannoplankton to both the total chlorophyll and primary production was quantified as a percent of the total for both parameters. In the absence of any consistent change in size segregation with depth, the values for each station were

averaged for the four depths and plotted against time of year (Fig. 5). Nannoplankton accounted for more than half the total chlorophyll during every station except May, and for more than half the primary production for every station except February and May. There is an indication of increasing nannoplankton influence from the spring through the summer, peaking in early fall with a minimum in winter.

Assimilation ratios ($\mu g\ C\ hr^{-1}\ (\mu g\ Chl\ a)^{-1}$) for both the total and nannoplankton were computed for each incubation. Assimilation ratios for the net plankton could be computed with sufficient accuracy only when there was an approximately equal distribution of both primary production and chlorophyll between the two size fractions. This occurred only in May. As can be inferred from the results in Fig. 5, the net plankton dominated primary production in February, thus the total plankton assimilation ratios may be considered a minimum measure of net plankton activity. For the remaining stations the nannoplankton dominated both primary production and chlorophyll and thus the total plankton assimilation ratios may be considered replicates of the nannoplankton values.

When the total or nannoplankton assimilation ratios for a given station are plotted against their mean incubation light intensities, the resulting distribution of points resembles a typical photosynthesis-light curve (Dunstan, 1973; McAllister et al., 1964). At low light levels there was a linear relationship between assimilation ratios and light intensity. As light levels increased further, assimilation ratios leveled off. The assimilation ratio-light intensity plots for the total plankton for each station and the net and nannoplankton for the February station are shown in Fig. 6.

With the apparent absence of photoinhibition at high light intensities the distribution of the observed data points can be described using the equation of Smith (1936) as modified by Talling (1957):

$$P = \frac{Pmax\ (I/I_k)}{(1 + (I/I_k)^2)^{\frac{1}{2}}}$$

where P is the assimilation ratio at light intensity I, Pmax is the light saturated assimilation ratio and I_k is a photosynthetic parameter expressing the light intensity at the onset of saturation (Talling, 1957). A value of I_k was calculated for each curve as the light intensity at the intersection of two lines representing Pmax and the initial slope of the curve (α) (Dunstan, 1973). Values of Pmax were calculated for each curve by averaging the light saturated assimilation ratios, and α was calculated as the initial slope of the curve restricted to passing through the origin. Values of Pmax, α and I_k for the total phytoplankton and nannoplankton for each station are shown in Table 2. The curves calculated from these values for the total plankton are shown in Figure 6. The goodness of fit between the experimental points and the generated curves was similar for the nannoplankton.

In August, a combination of low incident radiation and high turbidity resulted in *in situ* light levels insufficient to produce saturation for either the total or nannoplankton incubations. Consequently, values of Pmax were taken to be the mean of the assimilation ratios calculated from subsamples of the 11:00, 13:00 and 15:00 water samples for all four depths which were incubated under artificial light of saturating intensity (Warinner and Zubkoff, 1973). Saturation was not obtained for either the total or nannoplankton samples in June,

despite high *in situ* light levels. In this case, values of Pmax for each size fraction were calculated to minimize the deviations between the observed points and the calculated curve. The calculated values of Pmax were slightly higher and slightly lower than the maximum observed assimilation ratios for the total and nannoplankton respectively (Fig. 6). In February, light saturation was not achieved for the total plankton despite the fact that the nannoplankton were saturated at low light levels (Fig. 6). Pmax was determined for the total size fraction as in June.

Despite the general conformity of the observed assimilation ratios to the Smith equation curves, it was apparent that on certain dates the values were consistently higher in the afternoon than in the morning despite comparable light intensities. These deviations were quantified as the difference between the observed assimilation ratio and the value predicted by the Smith equation for that light level, expressed as a percentage of the predicted value. When the percent deviation for each sample was plotted against the midtime of its incubation, apparent diel patterns were observed at each depth. The results for the upper three depths for the total plankton for each station are shown in Figure 7.

In every case, except February, there was good agreement between the total and nannoplankton diel patterns at respective depths, another indication that these values reflect diel patterns rather than random variations. In many instances (May, August and November are the exceptions) the diel patterns are similar at all three depths. The aberrant 2.0 meter pattern observed in August reflects the relatively

low assimilation ratios at this depth (a result of low in situ light levels) which tend to exaggerate the magnitude of the deviations. For this reason, the 4.0 meter values were not included for any of the stations. The patterns for February, April, October and November indicate highest relative assimialtion ratios in the afternoon. The patterns for June and July indicate relatively high ratios in the morning and afternoon with a period of low values near midday. In May, a different pattern was observed at each depth. No apparent diel pattern was observed in August.

As a result of maximum assimilation ratios and maximum chlorophyll concentrations both occurring in the afternoon, rates of primary production were usually much higher during this part of the day than in the morning. The greatest difference was observed in April, when afternoon production rates were three times greater than midmorning rates, despite comparable light intensities.

Eppley (1972) suggests that temperature places an upper light on the magnitude of the assimilation ratio, and several investigators working in estuarine areas have observed correlations between light saturated assimilation ratios and temperature (Barlow, et al., 1963; Mandelli, et al., 1970; Williams and Murdoch, 1966). Consequently, the Pmax values for both the total and nannoplankton were plotted against their incubation temperature (Fig. 8). For comparison, the regression calculated by Williams and Murdoch (1966) for the Beaufort area estuary is also included. The York River values are generally lower at any given temperature than those predicted by the Williams and Murdoch line. In February, total plankton assimilation ratios

are considerably higher than would be predicted on the basis of temperature alone, while the assimilation ratios for May, July and August appear lower than would be expected on the basis of temperature.

DISCUSSION

The results of this study indicate that the nannoplankton contribute significantly to the primary production of the lower York River, and are in substantial agreement with recently published studies concerning nannoplankton in the Chesapeake Bay (McCarthy et al., 1974; VanValkenburg and Flemer, 1974) i.e., Nannoplankton normally accounts for 75-95% of both total primary production and total chlorophyll. No pronounced seasonal trends were observed in these values, although abrupt and substantial deviations do occur.

On the basis of their higher growth rates (Findenegg, 1965; Williams, 1964; Eppley and Sloan, 1966) one would expect the nannoplankton assimilation ratios to exceed those of the net plankton, and instances of this occurring have been observed in both marine (Malone, 1971a and b) and freshwater environments (Findenegg, 1965; Gelin, 1975; Kalff, 1972). Thus, the results of the February station are of particular interest both from the point of view that netplankton assimilation ratios so greatly exceed those of the nannoplankton and that netplankton assimilation ratios should be so high considering the low temperature.

Values of Pmax for the total plankton, similar to the February values found in this study, have been observed in the New York bight in January (T. C. Malone, pers. com.). These observations suggest that the biochemical limitation by low temperature is being circumvented either by the process of physiological adaptation or by the temporal

succession of a "cold adapted" species. Yentsch (1974) cites evidence which suggests that temperature adaptation by natural phytoplankton populations is more likely to occur by the second of these two processes, i.e. that temperature acts as a selective pressure. An indication that selection for a cold water form is taking place is found in the results of previous studies of the seasonal abundance of diatoms and dinoflagellates in the lower York River (Manzi, 1973; Mackiernan, 1968; Stofan, 1973). These studies all noted a distinct winter flora dominated by species indigenous to higher latitudes. Despite their high assimilation ratios relative to the nannoplankton, the net plankton in February still account for only 30% of the chlorophyll, suggesting that preferential grazing is limiting their biomass. The diel variation in the net plankton chlorophyll, compared to the nannoplankton for this station also indicates that the net plankton are the more dynamic size fraction (Fig. 3).

Considering the damped seasonal variation in chlorophyll abundances that is characteristic of the mid-to-lower Chesapeake Bay (Flemer, 1970; McCarthy and Taylor, 1974; Patten et al., 1963), the persistent diel variation in chlorophyll is of all the more interest. Diel variations in chlorophyll are frequently observed in aquatic systems (Glooschenko et al., 1972; Lorenzen, 1963; Yentsch and Ryther, 1957) and may result from a combination of a variety of factors including cell division (Jorgensen, 1966), chlorophyll bleaching (Glooschenko et al., 1972), grazing by zooplankton (McAllister, 1963; Wood and Corcoran, 1966) and changes in cellular chlorophyll (Yentsch and Scagel, 1958). The propensity of the nannoplankton to approximately double their minimum daily chlorophyll concentration (Fig. 4) suggests

that the increase may result from a phased division of cells with a doubling time of 24 hours. Generation times of 24 hours are common in microalgae (Bruce, 1965) and phytoplankton are easily synchronized for periodicity of cell division (Hasting and Sweeney, 1964). Synchronous mid-morning division by nannoplankton has been observed both in culture (Eppley et al., 1967) and in a natural phytoplankton assemblage (Sournia, 1968).

The occurrence of decreasing chlorophyll concentrations after rather than during maximum daily light levels suggests that bleaching is not the cause of the decrease. The occurrence of the decrease during or soon after the maximum photosynthetic rates indicates that insufficiency of substrate or presursurs for chlorophyll synthesis is not the cause of the decrease. Both of these factors have been implicated in diel variations of chlorophyll in coastal waters (Glooschenko et al., 1972). The most likely cause of the chlorophyll decrease observed in this study is zooplankton grazing. Diel periodicities in both zooplankton abundance and feeding are well known (Sameoto, 1975; McAllister, 1961; Ryther, Menzel and Vaccarro, 1961), and in a 24 hour study at this station in August 1973, net zooplankton were observed to reach peak concentrations in the upper 10 meters at dusk (G. C. Grant, personal communication).

In a previous study of the lower York River, Patten (1963) concluded that the summer phytoplankton community actively established and maintained a definite vertical distribution with respect to photosynthetic capacity. However, the observation that assimilation ratios measured at four different depths in the euphotic zone conformed to a single curve when plotted against light intensity indicates that the

phytoplankton in the euphotic zone are homogeneously distributed with depth with respect to their photosynthetic capabilities. This is probably a result of turbulent mixing within the upper mixed layer which exposes all phytoplankton to the same average environmental conditions, e.g. light, nutrients, temperature.

In a study in Oregon coastal waters, in situ assimilation ratios at suboptimal (less than saturating) light intensities were observed to vary with depth and time of day (Curl and Small, 1965). Since the assimilation ratios were plotted against percent incident light rather than absolute incubation light level, it is not possible to determine if the values for a given day would conform to a smooth curve. However, the fact that maximum assimilation ratios plotted against time of day described a symmetrical curve with maximum rates at noon, suggests that they would (Small et al., 1972).

The assimilation ratio-light intensity curves observed in this study are similar to those observed by McAllister et al. (1964) for several cultured marine algae, i.e. saturation usually occurred at 0.1 ly min^{-1} and no photoinhibition was observed at light levels as high as 0.4 ly min^{-1}. These results do not agree with those obtained by Ryther (1956) for a variety of algal species. He observed photoinhibition at light levels only slightly in excess of that needed to saturate photosynthesis. Photoinhibition has also been observed in near surface in situ incubations of natural phytoplankton (Curl and Small, 1965; Findenegg, 1965; Rodhe, Vollenweider and Nauwerck,, 1958) and incubation closer to the surface in this study may have produced similar results (0.5 meter incubations usually received 40-50% incident light intensity). However, the occurrence of photoinhibition in moored

surface incubations may not reflect the natural situation. In a turbulently mixed environment like the York River, it is unlikely that any cell would remain at any given depth for a period of time equivalent to an incubation, e.g. 2-24 hours. The absence of photoinhibition in this study may reflect a generally light adapted nature of the phytoplankton (Ryther and Menzel, 1959), which suggests that cells exposed to a constantly varying light intensity, in this case due to mixing, adapt to the higher rather than lower light intensities encountered.

Diel variation in photosynthetic rates is commonly observed in aquatic systems (Sournia, 1974). Most reports indicate that morning rates tend to be higher than those in the afternoon and attribute this effect to nutrient depletion in the afternoon (Malone, 1971a), or incomplete recovery from noontime photoinhibition (Harris and Lott, 1973). Higher afternoon rates have previously been observed in estuaries (Quasim et al., 1969; Sournia, 1968) and oceanic systems (Malone, 1971a). The relatively higher afternoon rates observed in this study may be related to the suggested cycle of phytoplankton division. Thus, morning metabolic processes may be geared more toward cell division than carbon fixation, or a higher proportion of physiologically "younger" cells in the afternoon may contribute to the higher rates.

The relatively depressed noontime assimilation ratios observed in June and July appear not to be the result of photoinhibition (Harris and Lott, 1973; Harris, 1973) despite their occurrence at or near maximum daily light levels. This conclusion is based on the observation that the noon depression in June occurred even though saturating light intensities were not attained at any of the incubation depths (Fig. 6). This suggests

that these depressions are endogenous rather than exogenous and thus similar to the "noon time nap" phenomenon often observed in terrestrial plants (Rabinowitch, 1951; Talling, 1961).

Comparison of the diel assimilation cycles in Fig. 7 suggests a seasonal cycle in their pattern. During short days (February and November) the diel variation results in a single peak at or soon after midday. On days of intermediate length (April and October) the single peak is shifted to a later hour, with an indication of both a secondary morning peak and a noon decrease. During the longest days (June and July) nearly equal mid-morning and mid-afternoon peaks are observed, separated by a period of relatively low values.

The results shown in Figure 7 suggest that the relationship between Pmax and temperature is not as well developed in this estuary as in the Beaufort area estuarine system (Williams and Murdoch, 1966). Of particular interest are the Pmax values for July and August, which are low even when compared to the June values at a similar temperature. These low values most likely reflect a mixed layer depth 5 to 6 times deeper than the euphotic zone. Consequently, the phytoplankton are subjected to a relatively low mean daily irradience and become shade adapted resulting in a lower level of light saturation (I_k). A comparison of α and Pmax values for June, July and August (Table 2) indicate that the decreased level of I_k observed during the latter two stations was primarily a result of a decrease in Pmax, since the magnitude of α is essentially identical for all three stations. This is in agreement with previous work which indicates that shade adaptation is accomplished through an alteration of the dark reaction rather than the light reaction of photosynthesis (Steemann-Nielsen and Hansen, 1959; Yentsch,

1974). Harris and Lott (1973) observed shade adaptation in natural photoplankton populations after only a few hours in low light. Therefore it is not unreasonable to expect shade adaptation in the relatively short time span during which deep vertical mixing occurs.

The effect of sun and shade adaptation on the magnitude of Pmax is well established (Harris and Lott, 1973; Ryther and Menzel, 1959; Stemann-Nielsen and Hansen, 1959; Yentsch and Lee, 1966) and the results of this study indicate that the degree of light adaptation can alter Pmax values by a factor or two, which is significant considering the small range of Pmax values generally encountered in nature (Eppley, 1972). Considering the relationship between the magnitude of Pmax and the depth of the surface mixed layer, a higher degree of sun adaptation and hence Pmax values, could presumably be achieved by a further reduction (within limits) of the mixed layer depth. In this regard, the generally higher Pmax values observed in the very shallow (mean depth 1.0 meter) Beaufort area estuaries (Williams and Murdoch, 1966) may be the result of a greater degree of sun adaptation. It is perhaps significant that the Pmax values observed during the April, June, October and Nov ber are from water columns with relatively shallow surface mixed layers relative to the depth of the euphotic zone, and that a line drawn through these points appears to parallel the values of Williams and Murdoch. There does not appear to be any hydrographically related reason for the low Pmax values observed in May.

During the summer of 1974, highly stratified conditions occurred on a biweekly cycle, in conjunction with the biweekly neap tides. A study of dissolved oxygen in the lower York River during this period (Jordan, 1974) revealed that levels of dissolved oxygen

far in excess of saturation were normally observed during these periods of stratification. The level of dissolved oxygen saturation can be used as a relative measure of the rate of primary production (Welch, 1969; Gelin, 1975). It appears therefore that the maintenance of high productivity in this deep estuary is dependent on a continued state of stratification. Thus, hydrographic factors may be having a considerable impact on plankton production.

The depth of the surface mixed layer has long been recognized as a significant factor in regulating primary production in coastal and oceanic environments (Gran and Braarud, 1935; Riley, 1952; Sverdrup, 1953). However, these same principles are rarely applied to estuarine plankton production because of the shallow, well mixed nature of most estuaries (Smayda, 1957). A close correlation between plankton production and vertical stability has been observed in a British Columbia fjord (Gilmartin, 1964), and the onset of a yearly phytoplankton bloom in the Duwamish estuary is apparently triggered by the occurrence of maximum water column stability (Welch, 1969; Welch et al., 1972). In the York River, periods of water column stability i.e. a shallow surface mixed layer, are characterized by high assimilation ratios compared to periods of mixing, and not by increased levels of chlorophyll. This may indicate that grazing is limiting the accumulation of biomass.

It has also been reported that the magnitude of the assimilation ratio is effected by nutrient availability (Curl and Small, 1965; Malone, 1971a; Thomas, 1970; McAllister et al., 1964), being lower under conditions of nutrient deficiency and higher under conditions of nutrient sufficiency. However, temperate estuaries are generally considered to be nutrient rich (Pomeroy 1970; 1975) and Eppley (1972) suggests that

the absence of nutrient limitation is the principal reason for the high correlations observed between temperature and assimilation ratios in these environments. Previous studies of nutrient (nitrogen) limitation in the Chesapeake Bay concluded that instances of nitrogen limitation are rare and that rapidly recycled forms of nitrogen (e.g. urea and ammonia) are preferentially utilized by the phytoplankton (Taylor, 1972; McCarthy and Taylor, 1974).

During the July, August, October and November stations, concentrations of ammonia and urea were measured periodically and rates of in situ urea utilization were measured in conjunction with the primary production samples. The results (Webb and Haas, 1975) during the July station indicate that measured rates of urea utilization were sufficient to supply all of the nitrogen needs of the phytoplankton. On all four occasions, ammonia concentrations were observed to undergo similar diel variations. Peak concentrations were observed in early morning. They decreased rapidly after sunrise, remained low throughout the day and increased again at night. The most pronounced diel variation occurred in October with daytime minimums of less than 1.0 μgat N l^{-1} and night maximums of about 4.0 μg-at N l^{-1}.

This diel variation in ammonia concentration suggests a periodicity in N assimilation rates with highest rates in the early morning. This may reflect a light dependent response to maximal early morning substrate concentrations or a temporal periodicity in ammonia assimilatory capacity. Similar periodicities have been observed both in culture (Eppley et al., 1971) and in natural plankton populations (Goering et al., 1964). Whatever the mechanism, maximum rates of ammonia assimilation appear to be out of phase with maximum carbon assimilation

rates, the latter occurring in the afternoon. Similar temporal relationships between carbon and nutrient assimilation have been demonstrated for phosphate in Lake George (Stross et al., 1973) and for ammonia in the Sargasso Sea (Goering et al., 1964).

The extent to which the diel variation observed for carbon assimilation is a phased (endogenous) oscillation entrained to a light dark cycle or a forced (exogenous) oscillation dependent upon ammonia availability in the morning is not known but presumably amenable to testing with the conceptual model of Stross et al. (1973). A temporal periodicity in nutrient assimilatory capacity, with uptake occurring in the early morning may explain the inconsistent repsonse obtained from nutrient enrichment experiments in the Chesapeake Bay in which enrichments were made near midday (Taylor, 1972).

The apparent ability of phytoplankton to markedly reduce ammonia levels, at times to concentrations less than 1.0 μg-at N l^{-1}, indicate that ammonia availability is a day to day proposition and dependent on a daily replenishment. This replenishment is most likely the result of zooplankton and/or microzooplankton (protozoan) excretion (Beers and Stewart, 1969; Johannes, 1968; Martin, 1965). The timing of the observed increase in ammonia coincides with the proposed period of maximum grazing. Thus, a closely linked relationship may exist between zooplankton grazing, nitrogen excretion and nutrient availability to the phytoplankton. High rates of nutrient regeneration within the surface mixed layer would seem to be necessary to maintain high rates of production, since stratification would largely eliminate nutrient input to the euphotic zone from the sediments and deep waters.

The similarities between the characteristics of the phytoplankton community and the proposed processes of regulation described for this estuarine environment and those observed in oceanic environments are worth noting. Characteristics normally attributed to oceanic phytoplankton communities include: domination of the phytoplankton by nannoplankton; limitations of biomass by grazing; diurnal variations in nutrient concentrations, metabolic function and biomass; a close coupling between zooplankton grazing and nutrient excretion; sun and shade adaptation; and regulation of primary production by hydrographic effects.

These similarities suggest that the dynamics of the phytoplankton community in this estuarine system and possibly others, are functionally similar to those in oceanic ecosystems but are operating on an order of magnitude higher level. The preceding interpretation admittedly involves much speculation, and the need for more research is apparent. However, the value of closely spaced measurements in estuarine research is apparent and should be employed whenever practicable. In this manner, it appears likely that the highly dynamic temperate estuarine ecosystem can be successfully analyzed and hopefully reduced to manageable terms.

Figure 1. Lower Chesapeake Bay and subestuaries with the location of the sampling station in the York River mouth.

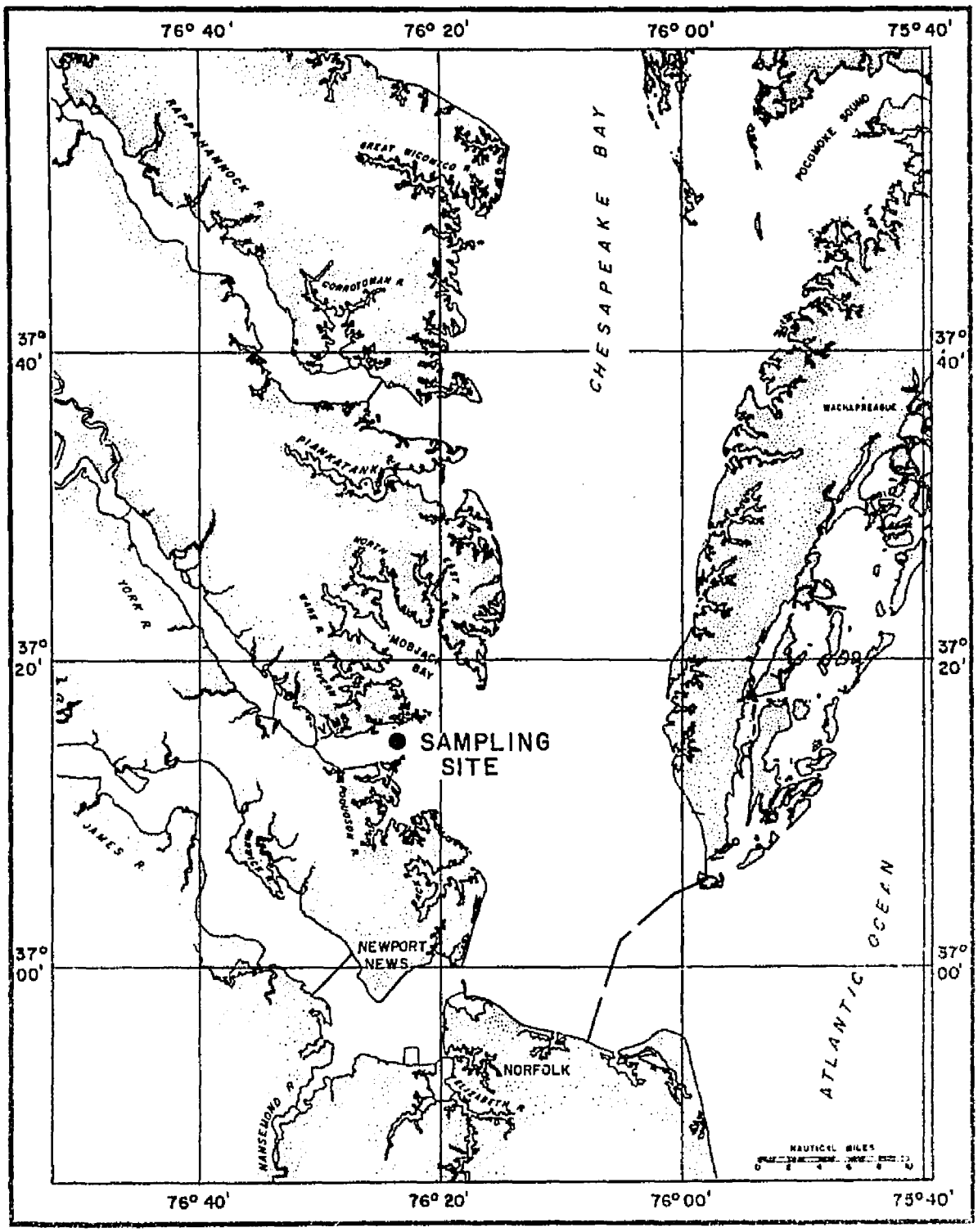
76° 40'
76° 20'
76° 00'
75° 40'
37° 40'
37° 20'
37° 00'
CHESAPEAKE BAY
RAPPAHANNOCK R.
CORROTOMAN R.
PIANKATANK R.
YORK R.
MOBJACK BAY
SAMPLING SITE
JAMES R.
POCOMOKE SOUND
WACHAPREAGUE
ATLANTIC OCEAN
NEWPORT NEWS
NORFOLK
NANSEMOND R.
NAUTICAL MILES

Figure 2. Pyroheliometer readouts (langleys min^{-1}) for the first day of each station. Total langleys per day appear below date.

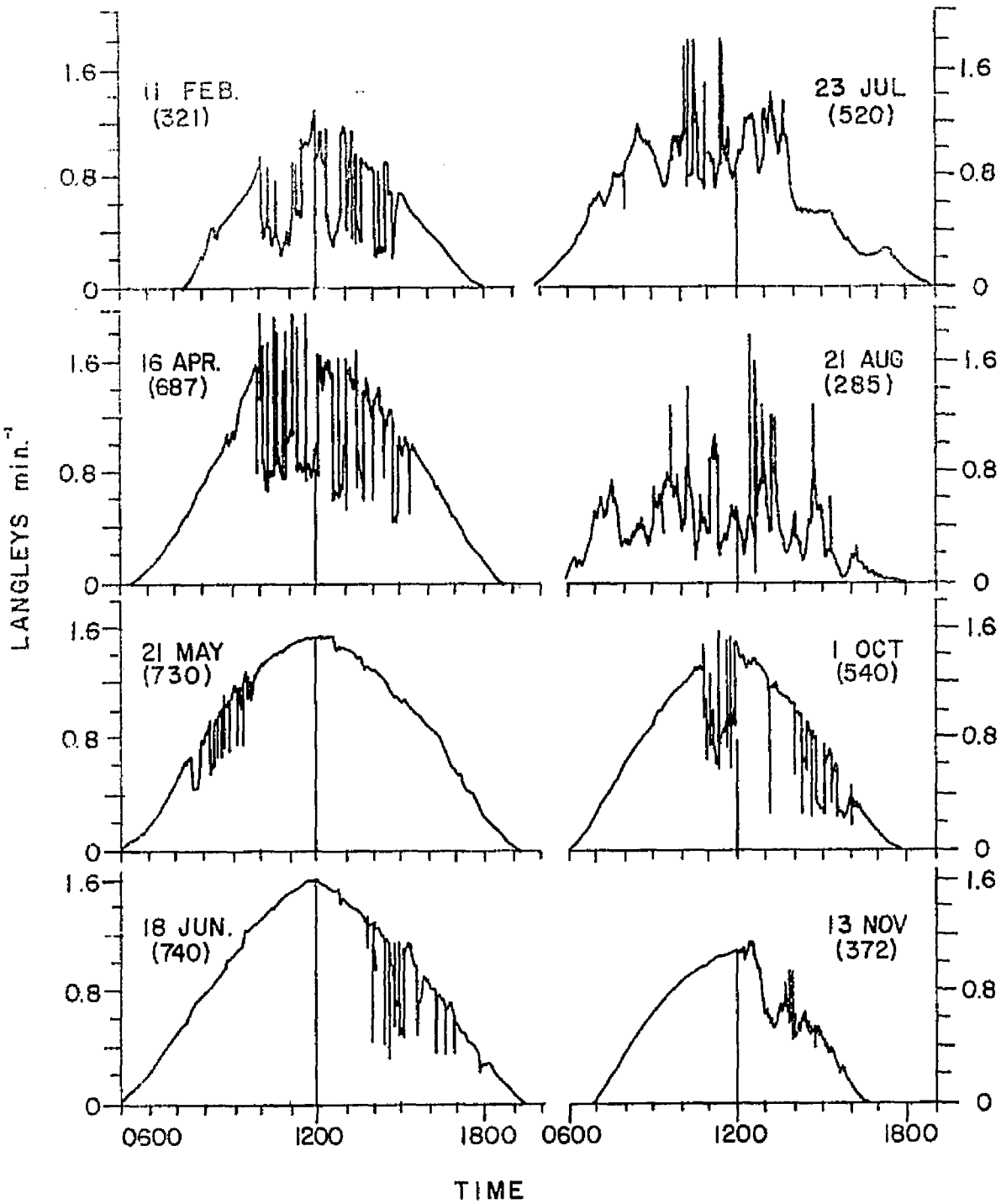
11 FEB.
(321)
23 JUL
(520)
16 APR.
(687)
21 AUG
(285)
21 MAY
(730)
1 OCT
(540)
18 JUN.
(740)
13 NOV
(372)
1.6
0.8
0
0600
1200
1800
LANGLEYS min.⁻¹
TIME

Figure 3. Total chlorophyll at time of sampling for each station. Values are the mean for the 0.5, 1.0, 2.0 and 4.0 meter depths. Bars include ± one standard error of the mean. Single points in April indicate only single sample (1.0 meters) taken. For February and May, net plankton (>15 µm; ———) and nannoplankton (<15 µm; ·····) concentrations also shown. Vertical columns indicate times that maximum (1200 - 1600) and minimum (0000 - 0400) chlorophyll concentrations normally observed. Times of high (▲) and low (▼) tide are indicated.

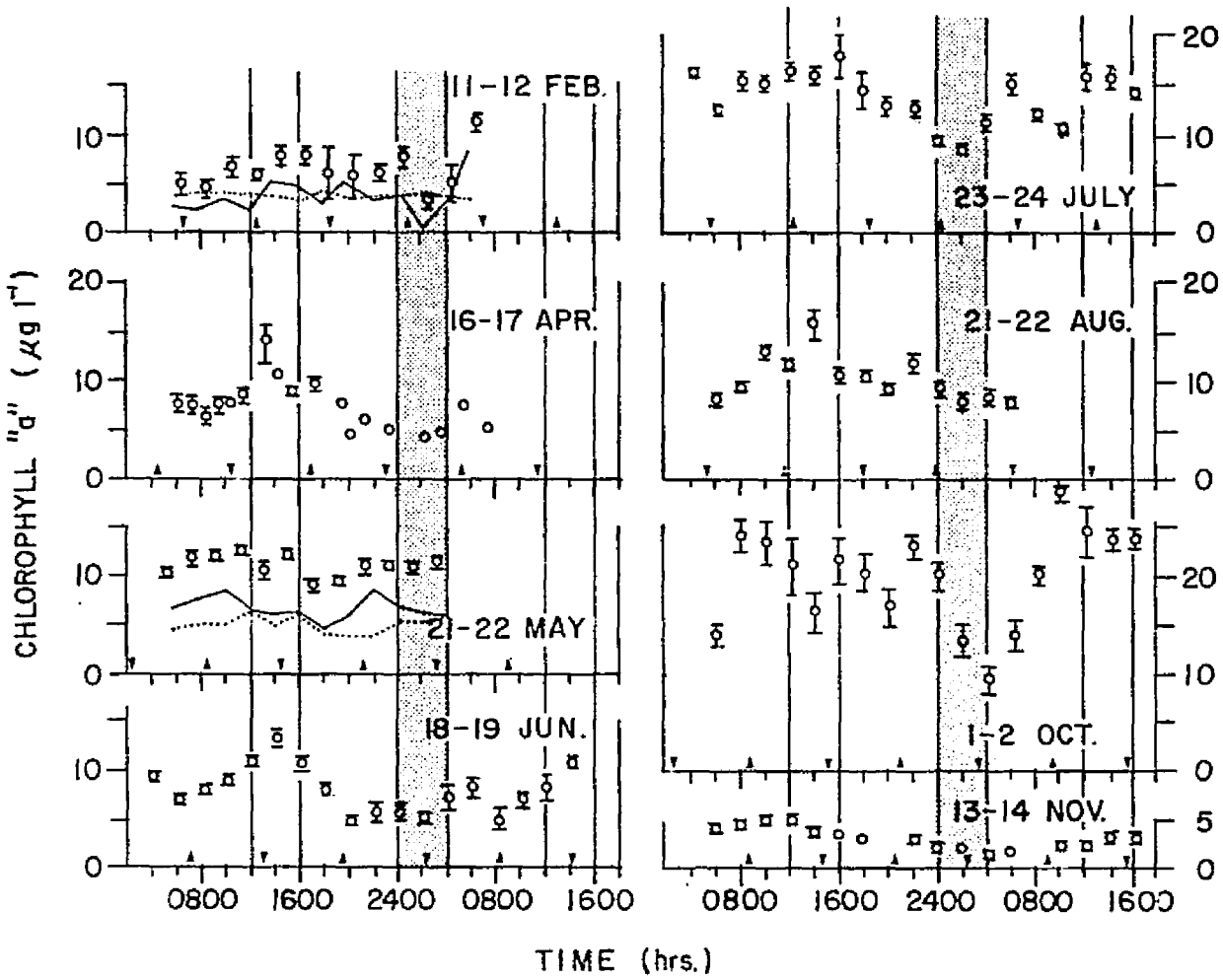
11-12 FEB.
16-17 APR.
21-22 MAY
18-19 JUN.
23-24 JULY
21-22 AUG.
1-2 OCT.
13-14 NOV.
CHLOROPHYLL "a" (μg l⁻¹)
TIME (hrs.)
0800
1600
2400
0800
1600

Figure 4. Diel variation in nannoplankton chlorophyll. Values are mean euphotic zone chlorophyll a concentrations expressed as a percent of the minimum daily value, and averaged for all stations excluding February and May (●——●). The number of observations are given in parentheses. Vertical bars indicate standard error of the mean. February data graphed separately (o----o).

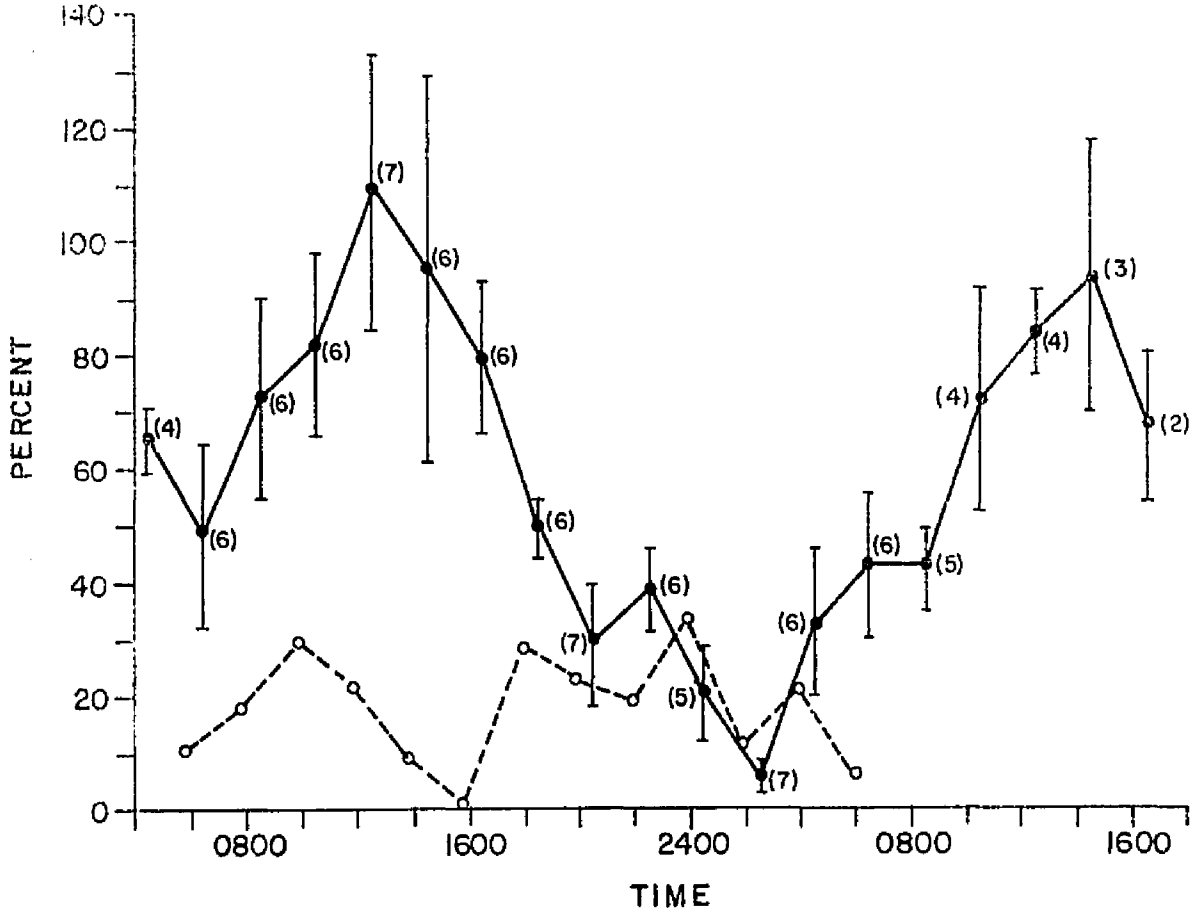
140
120
100
80
60
40
20
0
PERCENT
(4)
(6)
(6)
(6)
(7)
(6)
(6)
(6)
(7)
(6)
(5)
(7)
(6)
(6)
(5)
(4)
(4)
(3)
(2)
0800
1600
2400
0800
1600
TIME

Figure 5. Contribution of the nannoplankton as a percent of total chlorophyll a (●) and primary production (○). Values are averaged for 0.5, 1.0, 2.0 and 4.0 meters for all primary production incubations and all chlorophyll samples.

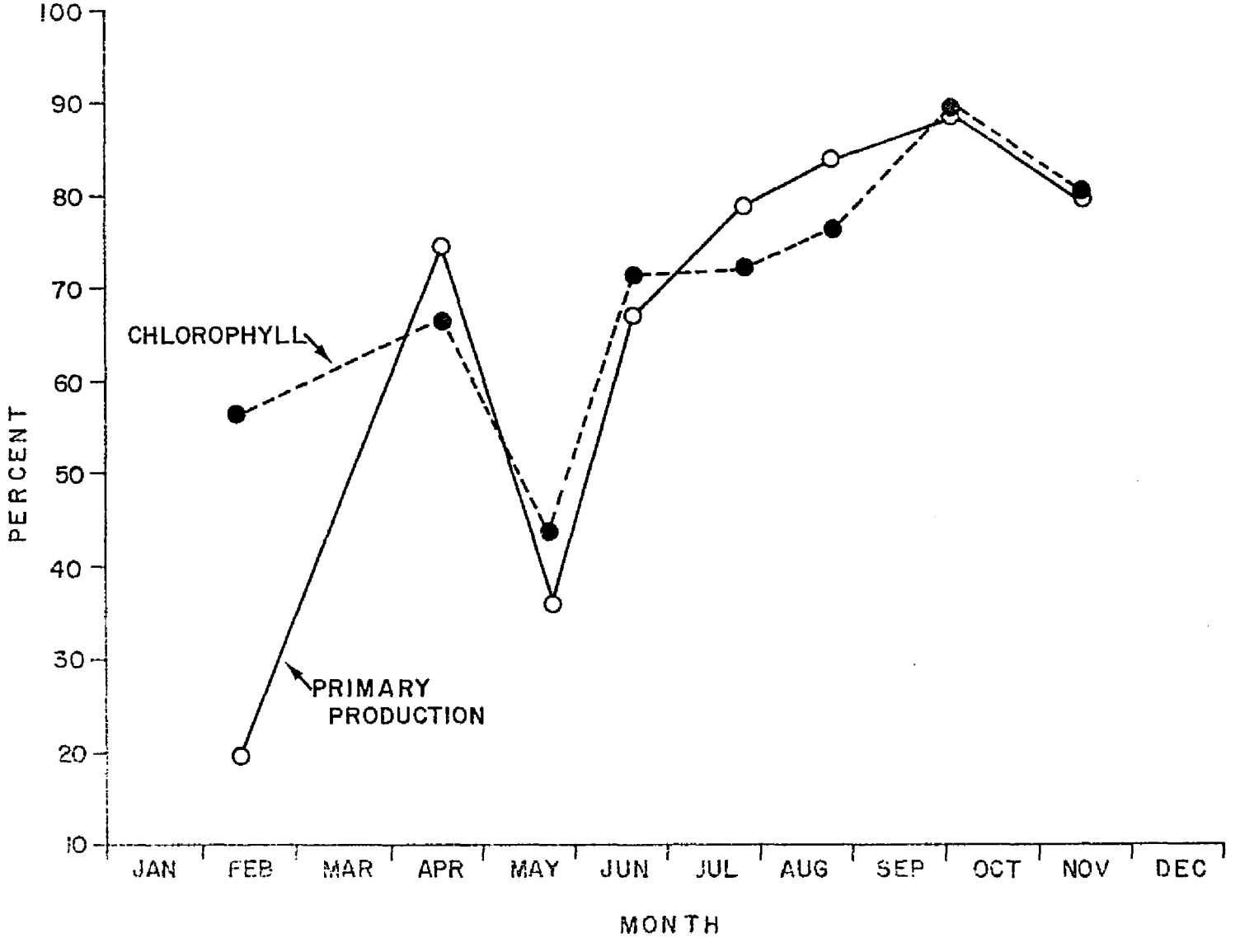
100
90
80
70
60
50
40
30
20
10
PERCENT
CHLOROPHYLL
PRIMARY
PRODUCTION
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
MONTH

Figure 6. Total phytoplankton assimilation ratios ($\mu g\ C\ hr^{-1}(\mu g\ Chl\ a)^{-1}$) plotted against mean integrated in situ light intensity (langleys min^{-1}) for each station (◦). For February the nannoplankton (<15 μm; o) and net plankton (>15 μm; ●) are also shown. Smooth curves drawn using data from Table 2. Estimated values of Pmax for February, June and August are shown (✱).

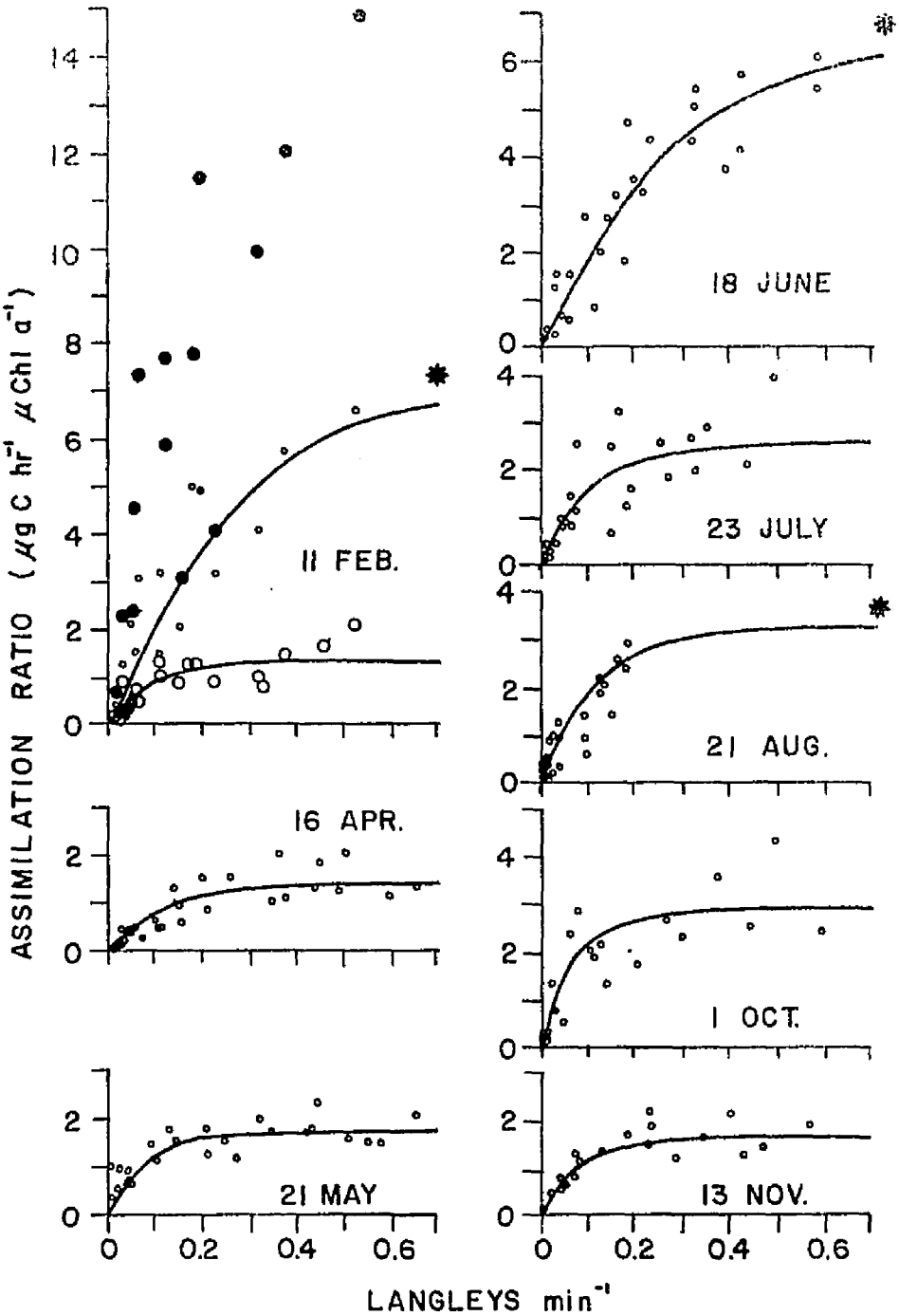
ASSIMILATION RATIO (μg C hr⁻¹ μChl a⁻¹)
11 FEB.
16 APR.
21 MAY
18 JUNE
23 JULY
21 AUG.
1 OCT.
13 NOV.
LANGLEYS min⁻¹

Figure 7. Diel variation in total phytoplankton assimilation ratios. Values are given as percent deviation from predicted value (smooth curves in Fig. 6) for 0.5 meters (——), 1.0 meters (·····), and 2.0 meters (----) and plotted against midtime of incubation.

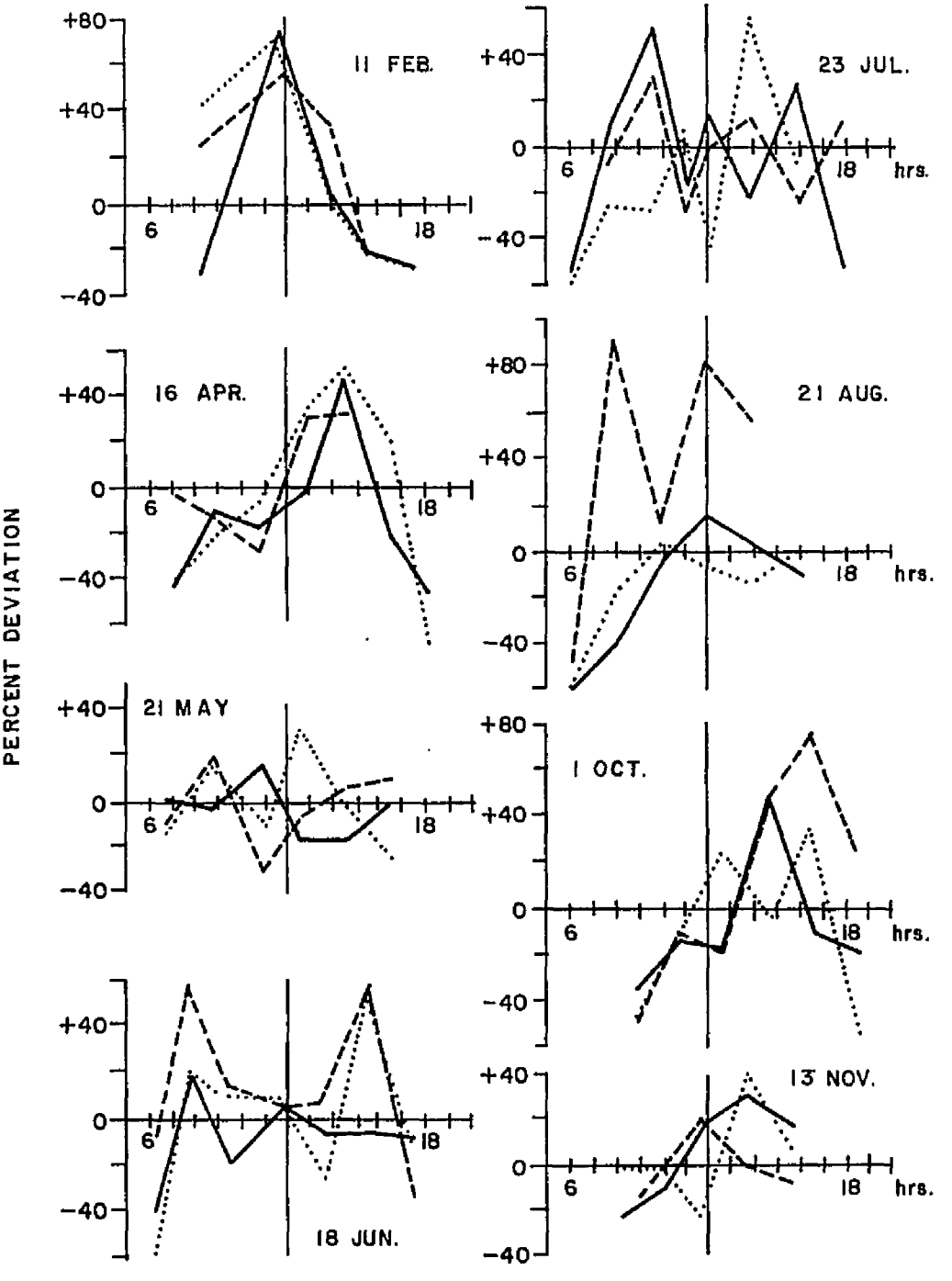
PERCENT DEVIATION
+80
+40
0
-40
6
18
hrs.
11 FEB.
23 JUL.
16 APR.
21 AUG.
21 MAY
1 OCT.
18 JUN.
13 NOV.

Figure 8. Total phytoplankton (●) and nannoplankton (O) light saturated assimilation ratios (Pmax) plotted against in situ incubation temperature. Smooth line is taken from Williams and Murdoch (1966) for the Beaufort area estuary.

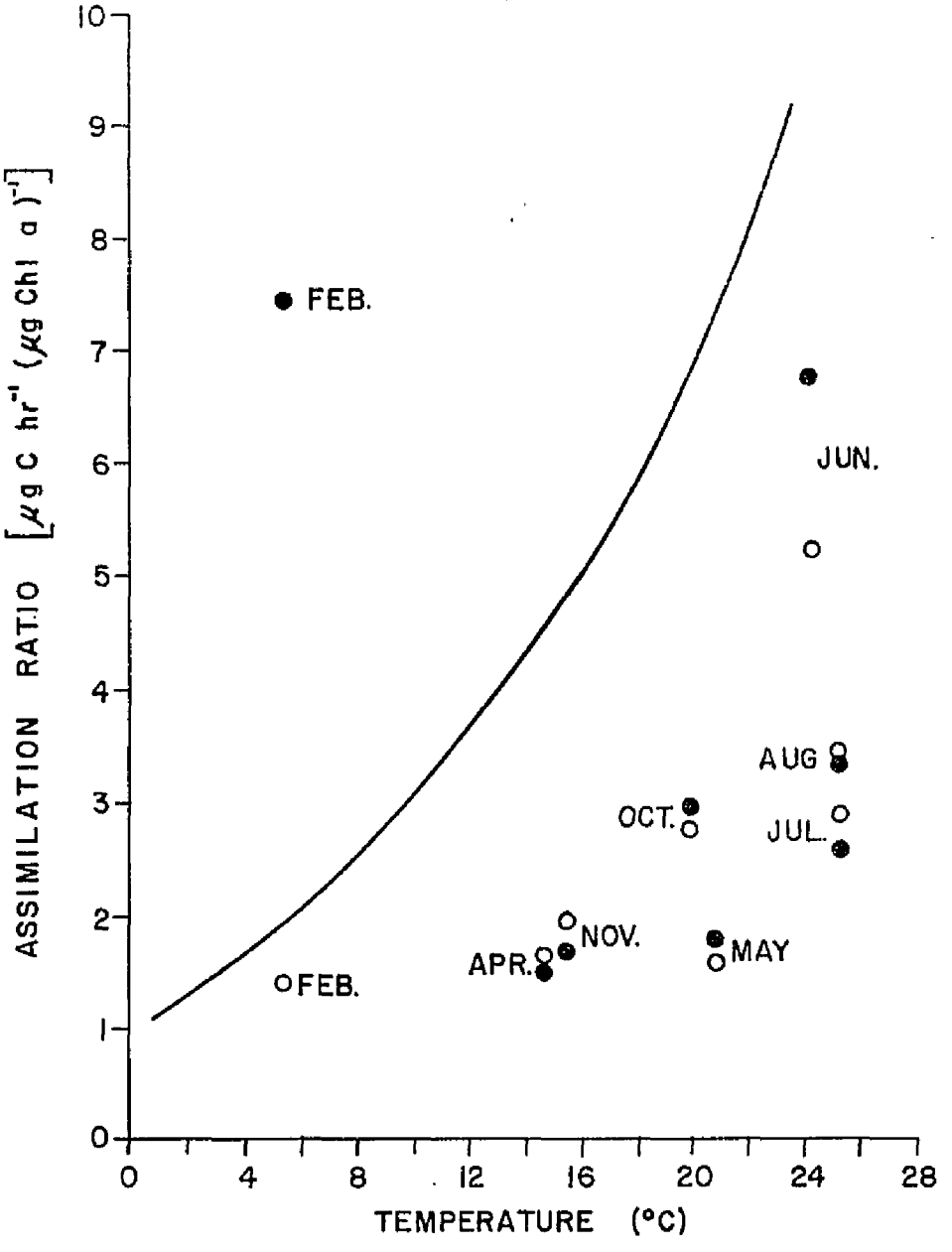
ASSIMILATION RATIO [μg C hr⁻¹ (μg Chl a)⁻¹]
TEMPERATURE (°C)
FEB.
JUN.
AUG
OCT.
JUL.
NOV.
APR.
MAY
FEB.
0
1
2
3
4
5
6
7
8
9
10
0
4
8
12
16
20
24
28

TABLE 1

Environmental data for eight stations. Values are means, with numbers of observations given in parentheses.

Date	Salinity (o/oo) Surface	Salinity (o/oo) Bottom	Salinity (o/oo) Δ	Temperature (°C) Surface	Dissolved O_2 (% sat.) Daily Max.	Dissolved O_2 (% sat.) Daily Min.	Mixed Layer Depth (m)	1% Light Depth (m)	Ext. Coeff. (m^{-1})	Ratio: MLD / 1% LD
11 Feb	17.11(9)	18.80(9)	1.71(9)	5.6(9)	99.0(3)	92.0(3)	14.3	7.0	0.66(7)	2.04
16 April	15.07(9)	25.25(9)	10.18(9)	14.7(8)	119.9(9)	104.3(6)	-	5.7	0.80(11)	-
21 May	16.45(9)	22.08(9)	5.63(9)	20.5(9)	116.2(9)	106.4(9)	9.2	5.8	0.79(10)	1.58
18 June	17.37(10)	26.26(10)	8.89(10)	24.3(10)	118.5(6)	100.7(9)	7.1	4.8	0.95(12)	1.47
23 July	20.41(10)	20.59(10)	0.18(10)	25.5(10)	92.9(7)	71.7(8)	18.0	2.9	1.59(8)	6.22
21 Aug	20.53(10)	20.60(10)	0.07(10)	25.4(10)	87.4(9)	76.6(9)	18.0	3.8	1.22(3)	4.74
1 Oct	20.29(9)	23.85(9)	3.56(9)	19.9(9)	106.0(9)	91.2(9)	10.4	4.3	1.08(8)	2.41
13 Nov	22.59(9)	23.67(9)	1.06(9)	15.6(9)	91.2(9)	87.7(9)	11.6	6.0	0.76(6)	1.93

TABLE 2.

Values of Pmax, α and I_k for the total phytoplankton and the nannoplankton (<15 µm) for each station. Values of Pmax are ± standard error of the mean. Number of observations given in parentheses.

	Pmax ($\mu gC\ hr^{-1}(\mu gChl\ a)^{-1}$)		α ($\mu gC\ hr^{-1}\mu gChl\ a^{-1})(ly\ min^{-1})^{-1}$		I_k ($ly\ min^{-1}$)	
Date	Total	<15 µm	Total	<15 µm	Total	<15 µm
11 Feb	7.50*	1.45±.22(5)	22.69 (11)	18.07 (8)	0.33	0.10
16 Apr	1.50±.14(9)	1.68±.18(9)	10.13 (8)	8.82 (7)	0.15	0.19
21 May	1.83±.10(9)	1.63±.11(8)	18.21 (7)	12.78 (9)	0.11	0.12
18 June	6.75*	5.25*	18.57 (16)	24.93 (9)	0.36	0.26
23 July	2.59±.27(7)	2.92±.36(5)	19.62 (12)	21.50 (12)	0.13	0.13
21 Aug	3.40±.26(12)+	3.47±.21(12)+	21.43 (18)	25.37 (18)	0.16	0.14
1 Oct	2.96±.33(6)	2.78±.14(4)	33.3 (9)	25.94 (7)	0.09	0.10
13 Nov	1.69±.12(9)	1.96±.17(9)	14.22 (8)	17.67 (9)	0.12	0.11

*Estimated for best fit.
+Mean of values incubated under artificial light.

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NUTRITIONAL MODE OF SEVERAL NON-PIGMENTED MICROFLAGELLATES FROM THE YORK RIVER ESTUARY, VIRGINIA

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ABSTRACT

Five species of non-pigmented microflagellates (3-10 μm), isolated from the York River, estuary, Virginia, U.S.A. were successfully cultured. All five microflagellates were shown, by feeding experiments and electron microscopy, to ingest live bacteria. These same microflagellates were not capable of utilizing 11 organic substrates at concentrations to 0.75 mg l^{-1}. I propose that the normal nutritional mode of the marine microflagellates tested is to ingest bacteria rather than dissolved organic matter or a combination thereof.

INTRODUCTION

The flux of dissolved organic matter (DOM) through the plankton ecosystem may represent a significant fraction of the carbon fixed via primary production (Pomeroy, 1974). Available evidence suggests that bacteria rapidly assimilate the more labile portion of this material (Wright and Hobbie, 1966; Andrews and Williams, 1971). The subsequent fate of these bacteria is generally unknown although Pomeroy (1975) and Andrews and Williams (1971) both speculate that grazing by bacterovorous protozoans is a likely possibility. One probable group of grazers, the obligately heterotrophic (non-pigmented) microflagellates, are however, close to bacteria in size (comparable surface area-to-volume ratios) and thus may compete with bacteria in membrane phenomenon such as DOM uptake by consuming DOM directly as well as indirectly through bacterial ingestion.

In this paper, I wish to report my results in attempting to evaluate the relative importance of two proposed pathways, DOM → bacteria → non-pigmented flagellates and DOM → non-pigmented flagellates.

MATERIALS AND METHODS

Isolation and Culture. Flagellates were isolated from the surface waters of the Lower York River at the Virginia Institute of Marine Science during June and July, 1969, with water temperature and salinity at 20-25C and 17-21 o/oo, respectively. The yearly temperature and salinity variation at this point in the river is 1-27C and 12-25 o/oo, respectively.

Aliquots of this water before and after plankton concentration (Dodson & Thomas, 1964) were placed directly into Erdschriebers enriched seawater medium (Butcher, 1959). In addition, individual flagellates were selected from the plankton concentrates by micropipetting and placed in the enriched seawater medium.

Cultures were grown in 50 ml of media in 125 ml erlenmyer flasks at 22-24C under light conditions used for culturing autotrophic organisms. After initial growth, further micropipetting and subculturing resulted in a variety of unispecific but non-axenic cultures of non-pigmented microflagellates.

Five of these microflagellates with their associated bacterial flora were successfully subcultured on a defined media similar to Provasolis'ASP6 (Droop, 1969) with glucose (1.0 gm l^{-1}) added as a carbon source.

Attempts to rid the microflagellate cultures of bacteria either by antibiotic treatment (Droop, 1967) or subculturing cells that had been repeatedly washed in sterile media were unsuccessful.

A variety of undefined and defined organic enrichments (amino acids, peptone, protein hydolysates) at concentrations as high as 5.0 g l^{-1} were used in an effort to provide growth substances apparently supplied by the bacteria. None were successful in permitting flagellate growth independent of bacteria.

In an effort to standardize the bacteria associated with the flagellates, aliquots from each flagellate culture were streaked out on 1% agar in the artificial seawater media. Three of the five cultures contained only one, albeit different, bacterial strain, while the remaining two yielded a fast and slow growing strain. Cultures of the five dominant bacteria (three single isolates plus two fast growing isolates) were initiated from the plates and the five flagellates, after washing in sterile media, were reinnoculated back into their respective bacterial associate. The final result was five unspecific flagellate-bacterial associations cultured in defined media.

The microflagellates used in this study were all biflagellate ovoid cells measuring 3-10 μm in diameter. Although no effort was made to identify to species, differentiation based on cellular and flagellar structure was possible (Fig. 2-4). The five bacterial strains used in this study were all gram-negative rods. Species differentiation was based on differences in cell morphology in liquid culture and colony morphology on agar plates.

Nutrition Experiments. Microflagellate ingestion of bacteria was assayed by observing the change in bacterial concentration and microflagellate numbers following the addition of microflagellates to post log phase bacterial cultures. Bacterial concentration was quantified

by the culture absorbence at 420 nm on a Spectronic 20 spectrophotometer and flagellate numbers were determined by counting with a standard hemacytometer and microscope.

Direct observation of bacteria ingested by microflagellates was possible by means of electron microscopy. Flagellate-bacterial cultures were fixed for 20 minutes with a 0.2 M cacodylate buffered 1% gluteraldehyde solution. The material was then pelleted with a clinical centrifuge and washed three times, ten minutes each time, in 0.2 M cacodylate buffer and autoclaved estuarine water (1:1) at pH 7.2. The material was then post-fixed with 0.1 M cacodylate buffered 1% OsO_4 for 2 hours, followed by rinsing with 0.1 M cacodylate buffer. After embedding in agar (2% in 0.1 M cacodylate buffer) the material was dehydrated in a graded acetone series and embedded in ACM resin. Thin sections were stained with 2% uranyl acetate followed by lead citrate and observed with a Hitachi HU-11B electron microscope.

In order to test for the uptake of dissolved organic material by the flagellates, the following method was used to separate them from their associated bacteria. Flagellates, from the flagellate-bacterial cultures, were innoculated into three day old cultures of their respective bacterial type. After a suitable growth period (3-5 days), the microflagellates were removed by sterile pipet from most of the remaining bacteria which tended to settle to the bottom. Further isolation consisted of concentrating the microflagellates by gentle centrifugation and resuspension of the pellet for 12 hours in fresh culture media containing 2500 $\mu g\ l^{-1}$ penicillin and 625 $\mu g\ l^{-1}$ streptomycin. The presence of glucose in the culture media was used to maintain the residual bacteria in an active metabolic state and thus susceptible

to the action of penicillin as suggested by Droop, (1969). The microflagellates were then washed twice with sterile media containing no glucose and resuspended at a concentration of 0.5 to $3x10^6$ cells ml^{-1} for use in the DOM uptake experiments. Samples of the test suspension were plated onto 1% agar in culture media with glucose before and after the uptake experiments to test for bacterial contamination.

The uptake and assimilation of dissolved organic substrates was determined following the techniques of Wright and Hobbie (1966). The following ^{14}C-labeled substrates were used in serial concentration ranging from 25 through 750 $\mu g l^{-1}$; L-alanine, L-aspartic, glycine, L-glutamic acid, L-leucine, L-serine, L-valine, L-threonine, glycerol, glucose and sodium acetate.

After incubation with the labeled substrate for 2-3 hours, the biological activity was stopped with formalin and the flagellates were filtered onto 25 mm, 0.50 µm Millipore^R EH filters prerinsed with culture media. The damp filters were placed in liquid scintillation vials with 200 µl NCS^R solubilizer for 24 hours. A toluene-based cocktail was added two hours or more prior to counting on a Beckman liquid scintillation counter, with a ^{14}C counting efficiency of about 90%.

RESULTS

Fig. 1 demonstrates the decrease in bacterial turbidity associated with the logarithmic increase in flagellate numbers when the latter are added to a post-log phase bacterial culture. Similar results were found when the same procedure was repeated with the remaining four flagellates.

Electron micrographs of sectioned flagellate-bacterial culture material confirmed bacterial ingestion by the flagellates. The food vacuoles of flagellates containing bacteria were easily visible (Fig. 6). Although no attempt was made to follow the digestion process of the ingested bacteria, food vacuoles with tightly packed membrane systems were observed (Fig. 7). These membrane systems were similar to those observed during the digestive process in cellular slime molds predatory on live bacteria (Hohl, 1965). Fig. 5 illustrates a flagellate apparently in the process of ingesting a filamentous bacteria. This physical association was observed often in cultures, with the flagellate adhering to the bacterial filament, more often than not at one end of the filament.

The results of the DOM uptake experiments demonstrated that, under the conditions described, the five flagellates were unable to take up any of the substrates tested. An uptake pattern resembling a hyperbolic function of the substrate concentration was only occasionally found and it was always associated with excessive bacterial contamination of the test material.

DISCUSSION

Considerable evidence suggests that up to 50% of primary production is channeled through the DOM pool of the marine environment. In a recent review, Pomeroy (1975) summarized one concept of how this DOM is returned to the particulate phase of the food web i.e. DOM → bacteria → phagotrophic protozoans. Data reported in this paper support this concept. Of the five non-pigmented marine flagellates studied, all were capable of ingesting and assimilating bacteria. Holozoic capabilities are apparently common among both pigmented and non-pigmented phytoflagellates (Boney, 1970; Lackey, 1967) and zooflagellates (Lackey, 1967).

I was surprised that the five flagellates studied appeared to be obligate phagotrophs and incapable of taking up DOM in the forms and under the conditions provided in this experiment. Hellebust (1970), Sloan and Strickland (1966), and Pope (1974) were unable to demonstrate any uptake capability in pigmented flagellates exposed to simple organic compounds at concentrations comparable to those used in this study. North and Stephens (1969) demonstrated the uptake of dissolved free amino acids (DFAA) by the pigmented flagellate *Platymonas subcordiformis* and contend that this uptake is a significant contribution to the nitrogen nutrition of this phototroph in the natural environment. I find their arguments unconvincing since they report an uptake constant (k_t) for glycine of 19 x 10^{-6} M l^{-1} which is about two orders of

magnitude higher than the glycine k_t for natural plankton populations (Hobbie et al., 1968; Crawford et al., 1974).

It seems unlikely that the concentration of antibiotics used in this experiment destroyed any uptake mechanisms for DOM since North and Stephens (1967) report that pretreatment of *Platymonas subcordiformis* for 24 hours with 0.4 g l^{-1} streptomycin had no effect on the uptake of DFAA. It is possible that using concentrations of substrates higher than 0.75 mgl^{-1} might result in uptake. Eight marine ciliates have been cultured in defined media utilizing individual amino acids in concentrations ranging from 0.1 to 1.2 gl^{-1} (Hanna and Lilly, 1974; Soldo and Merlin, 1972).

Without additional experimentation (in culture and *in situ*), it is difficult to evaluate the ecological significance of bacterial grazing by flagellates. The extent to which flagellates in nature can graze all bacteria or whether they are restricted to specific bacteria is unknown. Hardin (1944) demonstrate that flagellates are capable of grazing 38 different strains of bacteria and Pomeroy (1974) speculates that they may even ingest smaller pigmented flagellates. In any case, ingestion of smaller particles by larger particles allow materials, that might otherwise have been lost due to their small size, to be available to the higher trophic levels.

The extent to which bacterial numbers in the marine environment are regulated by flagellate grazing is unknown. This may be especially significant in environments subjected to contamination by sewage where bacterial numbers are high and certain species of zooflagellates are known to thrive (Lackey, 1967).

The contribution of protozoans to nutrient regeneration in the marine environment is likewise unknown. Pomeroy (1970; 1974) speculates that they and not bacteria may be the primary agents of nutrient regeneration, and Johannes (1964; 1965) demonstrated their effectiveness in phosphorus regeneration. Barsdate et al. (1974) have reported higher levels of ammonia in bacterial-detritus cultures grazed by protozoans than in similar cultures with no grazers, indicating a possible role in nitrogen regeneration for protozoans.

Some measure of the contribution of the non-pigmented flagellates to the metabolism of the marine environment may be gained from observations of their relative abundance. Several investigators have noted large populations in marine environments (Reid, 1972; Wood, 1963a&b). The observation by Pomeroy and Johannes (1966; 1968) that a significant fraction of the respiration measured in the Western North Atlantic, Gulf Stream and Sargasso Sea can be accounted for by non-pigmented flagellates on the order of 5-10 μm in size further supports the concept that they constitute a major pathway through which energy flows and nutrients cycle. Confirmation of this hypothesis awaits the development of *in situ* techniques to quantify their contribution to the metabolism of the marine environment.

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Figure 1. Growth of bacteria (○) and microflagellate 8CA (●) in culture media. Bacteria innoculated at 0 hrs. and microflagellates added to bacterial culture at 303 hrs.

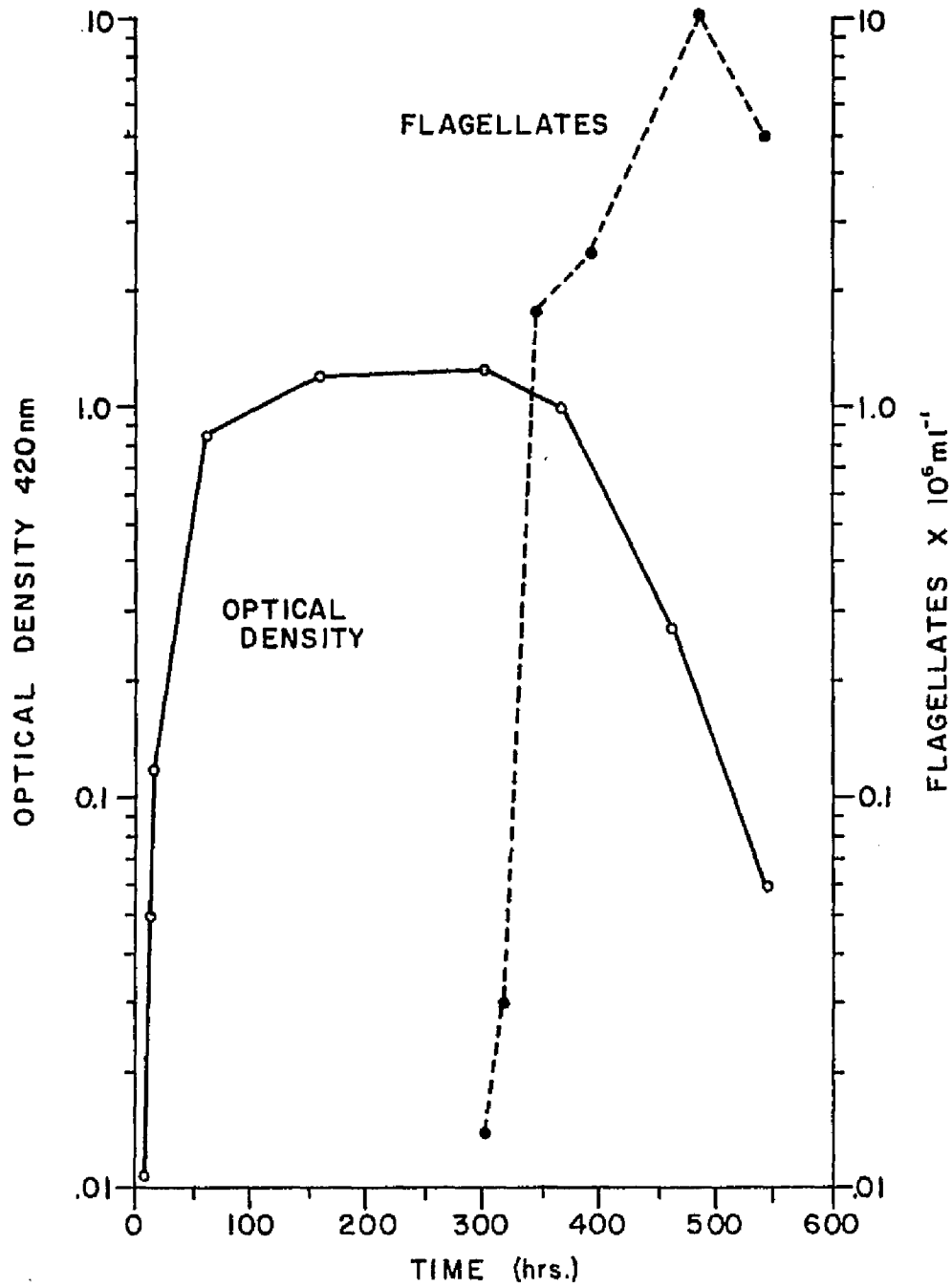
10
1.0
0.1
.01
FLAGELLATES
OPTICAL DENSITY
OPTICAL DENSITY 420nm
FLAGELLATES X 10⁶ml⁻¹
0
100
200
300
400
500
600
TIME (hrs.)

Figure 2. Whole mount of flagellate 6A. Bar equals 1.0 µm. Fixed with fumes generated from 2% osmium tetroxide and shadowed with platinum-palladium.

Figure 3. Whole mount of flagellate 9C. Bar equals 1.0 µm. Fixed as in Fig. 2.

Figure 4. Whole mount of flagellate 8CA. Bar equals 1.0 µm. Fixed as in Fig. 2.

Figure 5. Flagellate 8CA engulfing bacterial filament. Bar equals 1.0 µm. Fixed as in Fig. 2.

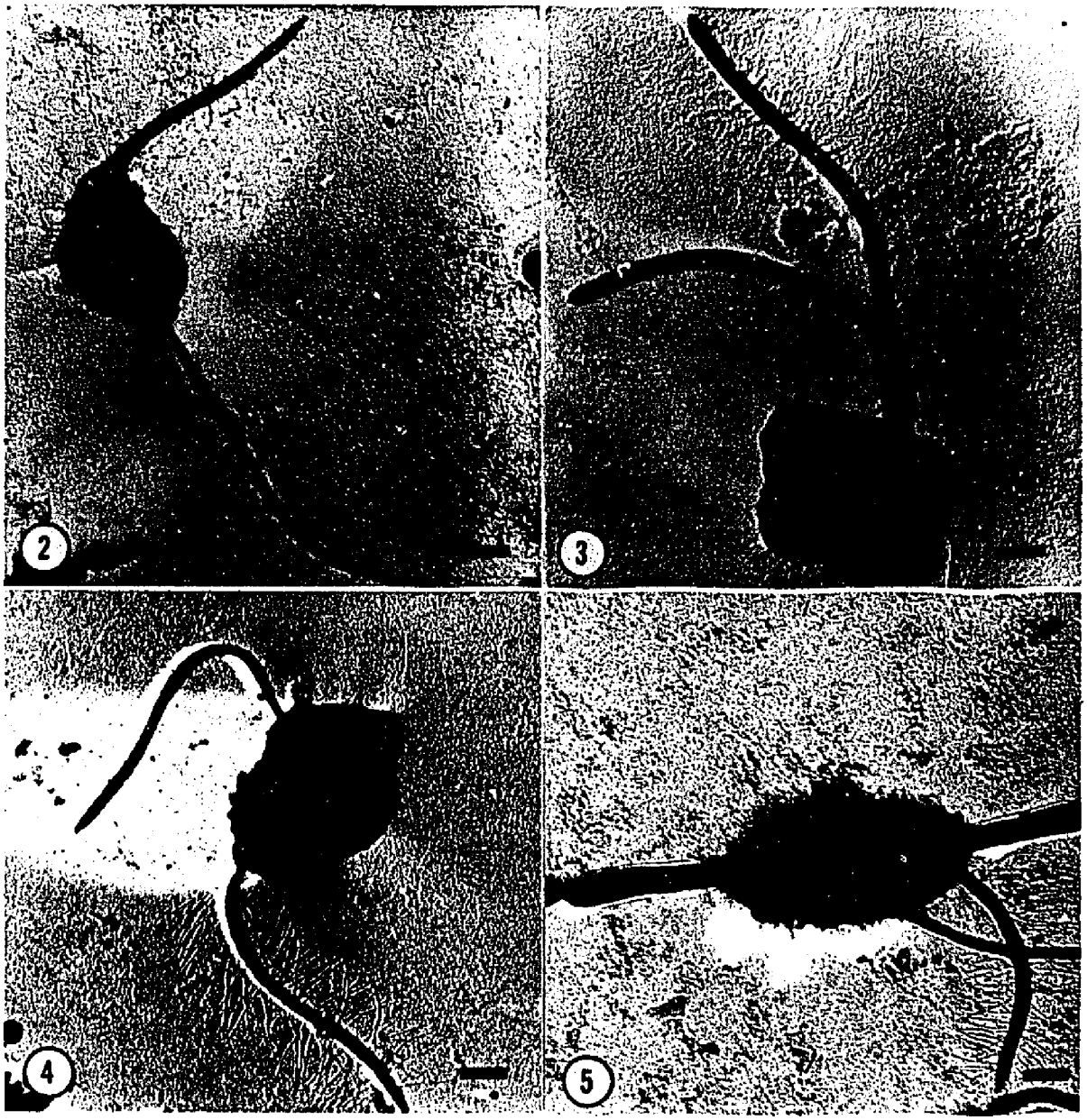
2
3
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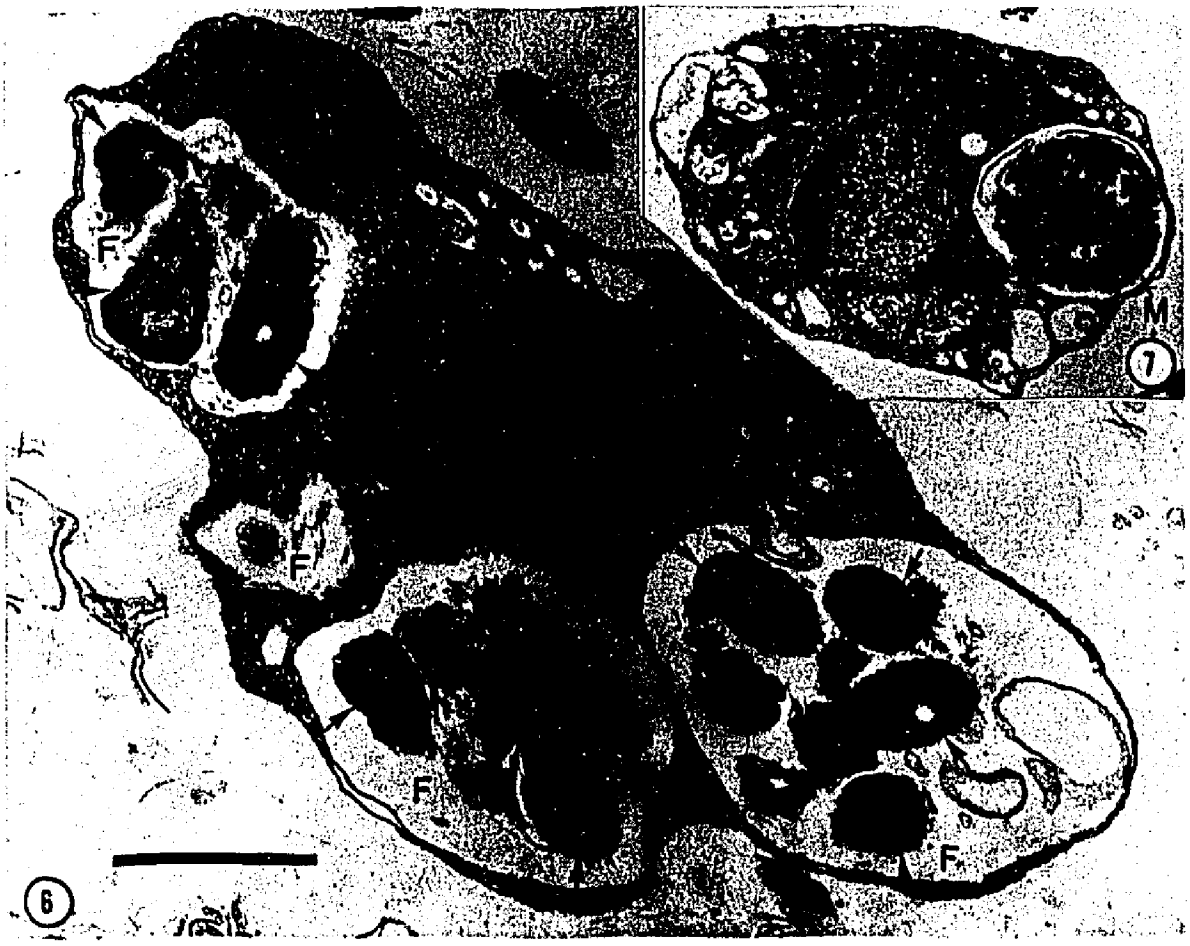
Figure 6. Flagellate 8CA with food vacuoles (F) containing bacteria (arrows). 28,000X. Bar equals 1.0 µm.

Figure 7. Flagellate 8CA with food vacuole containing packed membrane system (M). 15,125X.


F
F
F
F
M
6
7

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CONCLUSION

The results of this study indicate that an active and dynamic phytoplankton community exists in the lower York River. This was particularly manifest in the short term (hourly) variations observed in several biological parameters. Persistent diel cycles were observed in chlorophyll concentration (highest in mid-afternoon and lowest near midnight) and assimilation ratio (highest in midmorning and/or mid-afternoon depending on the day length). Ammonia concentration also exhibited a dramatic diel cycle (highest in early morning, lowest at midday) (Webb and Haas, 1975). Available evidence suggests that diel cycles also exist for nannoplankton division (synchronously during early morning), ammonia assimilation (greatest in early morning), ammonia production (greatest in late afternoon and evening) and herbivore abundance and/or feeding activity (greatest in late afternoon and evening).

The hypotheses advanced to explain these diel vairations are in substantial agreement with the compartmental model shown in Figure 1 (Introduction) and are summarized as follows. The nannoplankton dominate primary production, synchronously dividing in the early morning hours. Ammonia assimilation by phytoplankton is apparently keyed to the availability of light in the morning, and relatively high ambient concentrations of ammonia are markedly reduced by noontime. Rates of urea utilization indicate that it is, at times, a significant source of

nitrogen for the phytoplankton. Light energy is apparently more effectively directed toward the process of photosynthesis in the afternoon, generally resulting in highest assimilation ratios at this time. The accumulation of phytoplankton biomass is reduced by herbivore grazing which apparently occurs at maximum rates in the late afternoon and early evening. During the same period, ammonia concentrations increase presumably a result of zooplankton excretion. Thus, it is proposed that a close interaction exists between the phytoplankton and zooplankton, mediated by the processes of both grazing and nutrient regeneration and utilization.

The need for further documentation of the preceding hypotheses is apparent. The first experimental priority for further research would appear to be periodic (several times daily) determination of nannoplankton numbers so that the nature of the diel variation in chlorophyll abundance can be determined. Similarly, concurrent quantification of zooplankton abundance and/or feeding activity is necessary to substantiate the proposed cause for the daily decrease in chlorophyll abundance and the increase in ammonia concentration.

The results of this study also suggest that the biological and physical parameters regulating primary production in the lower York River are varied and include temperature, zooplankton grazing, light availability and hydrographic conditions.

The relationship between primary production and temperature in this ecosystem follows a pattern similar to that observed in other temperate estuaries i.e. a positive correlation between temperature and the light saturated rate of photosynthesis (Pmax) resulting from the effect of temperature on the dark or biochemical reaction of photo-

synthesis. In this instance, however, the correlation is partially obscured by two factors. The occurrence of shade adapted phytoplankton throughout the euphotic zone during periods of vertical homogeneity (mixed layer depths 5-6 times greater than the euphotic zone depth) resulted in Pmax values 50% of those observed at comparable temperatures during periods of stratification. The apparent selection of cold adapted net phytoplankton species in February resulted in assimilation ratios considerably higher than would be predicted on the basis of temperature alone. Similar observations of high winter assimilation ratios in the New York bight (T. C. Malone, pers. comm.) and an indication of the same phenomenon in the upper Chesapeake Bay (VanValkenburg and Flemer, 1974) suggests that selection for cold adapted phytoplankton in temperate estuaries may be a relatively common occurrence and warrants further investigation.

Regulation of primary production by light availability apparently operates in both a direct and indirect fashion. Direct regulation is apparent in the hyperbolic nature of assimilation ratio versus light intensity curves, when data from all depths of the euphotic zone are combined. This suggests that the phytoplankton are homogeneously distributed in the euphotic zone with respect to photosynthetic capability, and that the photosynthetic rate of natural phytoplankton assemblages does conform to incident light intensity in a predictable manner. The former conclusion is contrary to that arrived at by Patten (1963) for York River phytoplankton, and Curl and Small (1965; see also Small, Curl and Glooschenko, 1972) apparently overlooked the latter point in a study of phytoplankton photosynthesis off the Oregon Coast.

The indirect regulation of primary productivity by light is manifest in conjunction with the variable hydrographic condition described for the York River. The relatively deep water column in this estuary combined with a shallow euphotic zone, characteristic of turbid estuaries, provides the appropriate conditions for phytoplankton to become shade adapted (e.g. decreased values of Pmax) when the water column becomes vertically homogeneous. The effect of this shade adaptation on the annual primary productivity of the system will have to await more detailed studies concerning both the amount of time during the summer that the estuary is vertically homogeneous and the amount of time necessary for the phytoplankton to become sun or shade adapted once appropriate conditions are established. However, considering that shade adaptation can decrease rates of Pmax by 50% and that periods of vertical homogeneity should theoretically be both more numerous and of longer duration in the summer, when assimilation ratios are potentially highest, suggests that shade adaptation could have a potentially significant effect on the total annual rate of production.

The regulation of phytoplankton biomass by herbivore grazing is suggested by two observations: the relatively damped seasonal fluctuation in chlorophyll abundance in the lower Chesapeake Bay observed by previous investigators (Flemer, 1970; McCarthy and Taylor, 1974); and the late afternoon decrease in chlorophyll abundance coincident with the daily increase in ammonia concentration. As was noted previously, the validity of the latter observation needs to be confirmed by further research. However, the domination of primary production by nannoplankton suggests that the dominant herbivores may not be the net zooplankton traditionally sampled in zooplankton studies. It is suggested

therefore that in subsequent studies concerning zooplankton abundance, more attention be accorded to the smaller zooplankton forms (i.e. micro-zooplankton) such as ciliates, rotifers and microflagellates.

The observation that both urea and ammonia assimilation are light dependent (Webb and Haas, 1975) suggests that during the periods of this study, the York River phytoplankton were not nutrient starved. However, this study does raise some potentially interesting questions concerning the interaction between phytoplankton physiology and nutrient availability. For example, do the phytoplankton retain the capacity to assimilate ammonia and urea throughout the light period or is this capability restricted to only a particular part of the day? Are the temporal characteristics of nutrient assimilation capacity similar for the more abundant species or does it vary widely from one species to another (Stross and Pemrick, 1974)? To what extent are the processes of cellular division and peak afternoon assimilation ratios dependent upon an adequate supply of nutrients or are these physiological processes largely endogenous in nature (Stross, Chisholm and Downing, 1973)? Several studies have indicated that the assimilation and reduction of nitrate by phytoplankton is inhibited by concentrations of ammonia exceeding about 1.0 µg-at N l^{-1} (McCarthy and Taylor, 1974; Pomeroy, 1970). Considering the daily range of ammonia concentrations observed in the lower York River (0.5 - 4.0 µg-at N l^{-1} on 1 October) and the short term nature of its cyclic variation, it would be interesting to know if the capability of the phytoplankton to utilize nitrate is turned "on and off" on such a short time scale. Further research pertaining to these questions might conceivably elucidate mechanisms of competitive interaction between phytoplankton in this ecosystem. One experimental

approach might be to note the appropriate physiological response of the phytoplankton under altered nutrient conditions produced either by isolating the phytoplankton from the environment at certain times of the day or by nutrient additions to phytoplankton samples at appropriate times of the day.

Hydrographic conditions in the York River are unique, and their effect on primary production, through the process of sun and shade adaptation, has been noted. However, other questions are raised concerning the effect of this variable but predictable hydrographic cycle on the phytoplankton community. The results of this study indicate that periods of intense stratification do not result in greatly increased levels of chlorophyll as has been reported for other estuaries (Welch, 1969; Gilmartin, 1964) and coastal areas (Gran and Braarud, 1935; Riley, 1952), despite relatively high Pmax values, compared to periods of vertical homogeneity. Other regulatory mechanisms (grazing?) are apparently limiting the accumulation of phytoplankton biomass under what appear to be favorable hydrographic conditions for a bloom. Although no red tides were observed during any of the eight stations, they frequently occur in the lower reaches of the tributaries of the Chesapeake Bay. It is possible that the sudden occurrence and dissipation of red tide conditions in these tributaries is related to the observed cycle of stratification and mixing in these estuaries.

The cycle of stratification and mixing may also play a role both in regulating the availability of nutrients to the euphotic zone and the process of species succession in these estuaries. Under stratified conditions, nutrients regenerated in the sediments cannot reach the surface waters, and might be expected to build up in the deeper waters.

Under anaerobic conditions, which frequently occur in the summer (Jordan, 1974), onemight expect a buildup of ammonia in the bottom waters (Gelin, 1975). during subsequent periods of mixing these nutrients may be mixed into the euphotic zone and made available for photosynthesis. Following a period of vertical homogeneity, stratification is reimposed by the intrusion of high salinity ocean water along the bottom of the estuary. New species of phytoplankton may be brought in to the estuary in this high salinity water, but do not become apparent until a period of vertical mixing introduces them into the euphotic zone. In this manner, the appearance of new species may be regulated by the processes of stratification and mixing.

A distinct advantage in studying the interaction between hydrography and biology in the lower York River is the inherent predictability of the stratification-mixing process. As result, studies can be planned to include one or the other or both hydrographic conditions and the past history of the biota can be surmised. Few, if any, other marine ecosystems can offer such divergent hydrographic conditions over so short a time period, with the added advantage of predictability, as the York River.

The nutritional studies with the non-pigmented microflagellates indicate that despite their obligately heterotrophic nature, they apparently do not compete with bacteria for dissolved organic carbon (pathway 5b, Fig. 1., Introduction). Rather, these organisms appear to be a likely pathway by which carbon, nitrogen and phosphorus contained in bacterial biomass is made available to higher trophic levels of the food web (9a, Fig. 1). Two areas of further research are immediately apparent. The first is to develop suitable techniques to quantify in

situ rates of bacterial grazing by microflagellates. The second is to investigate the potentially significant role these organisms might play in the regeneration of nitrogenous nutrients in the plankton ecosystem (2a, Fig. 1).

The purpose of this study was to identify and quantify the basic parameters of the lower York River plankton community. Relative success was achieved in elucidating the dominant phytoplankton component, some of the primary pathways of energy flow and nutrient flux, and the major biological and physical factors regulating this community. A predictive capability vis-à-vis man's continued impingement on and alteration of this environment is probably still not possible, and will probably not be a reality until interaction among all trophic levels is considered.

The perhaps inevitable result of this study was to raise more questions than were answered. However, it does indicate that the biological characteristics of the lower York River plankton community are amenable to intensive short term studies, and it is hoped that as a result, additional and more detailed investigations will take place.

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APPENDIX A

Salinity and tide data from the lower York and Rappahannock Rivers for 1974.

Table A1. Salinity and tide data from the lower York River for 1974. Date, station, surface and bottom salinities, surface-to-bottom salinity differences (Δ), mean daily predicted high tide height (H), and mean daily tide range (R) are shown. Values of H and R are shown for same day as the salinity observation (0) and for each of the five days prior to that (-1, -2.....-5). Values of both H and R are given in feet for Hampton Roads, Virginia. To convert to meters for the lower York River subtract 0.2 and divide by 0.3048. A description of the station designations and locations are given below.

Station #		N. latitude	W. longitude
1	Biological station "B"	37°14'40"	76°23'28"
2	Jordan's (1974) station I-3	37°14'42"	76°23'30"
3	Jordan's (1974) station II-2	37°14'14"	76°25'43"
4	Jordan's (1974) station III-2	37°13'54"	76°27'20"
5	Jordan's (1974) station IV-2	37°14'00"	76°29'13"
6	Jordan's (1974) station V-1	37°14'21"	76°30'20"
7	Physical Oceanography slack water station Y0.0	37°14'50"	76°23'12"
8	Physical Oceanography slack water station Y3.6	37°14'00"	76°27'30"
9	Physical Oceanography slack water station Y4.8	37°14'00"	76°29'06"

Date	Station	Salinity (o/oo)			High Tide Height (ft.)						Tide Range (ft.)					
		Surface	Bottom	Δ	0	-1	-2	-3	-4	-5	0	-1	-2	-3	-4	-5
1801	7	16.95	20.23	3.28	1.95	1.95	2.05	2.10	2.25	2.40	2.04	2.02	2.12	2.34	2.60	2.88
1801	8	16.21	19.96	3.75	1.95	1.95	2.05	2.10	2.25	2.40	2.04	2.02	2.12	2.34	2.60	2.88
1801	9	16.18	18.83	2.65	1.95	1.95	2.05	2.10	2.25	2.40	2.04	2.02	2.12	2.34	2.60	2.88

Table A1 (Continued)

Date	Station	Salinity (o/oo) Surface	Bottom	Δ	High Tide Height (ft.) 0	-1	-2	-3	-4	-5	Tide Range (ft.) 0	-1	-2	-3	-4	-5
1102	1	17.11	18.82	1.71	2.50	2.62	2.75	2.85	2.80	2.75	2.94	3.22	3.48	3.66	3.62	3.46
1202	1	17.11	22.40	5.29	2.30	2.50	2.62	2.75	2.85	2.80	2.60	2.94	3.22	3.48	3.66	3.62
1202	7	16.30	19.11	2.81	2.30	2.50	2.62	2.75	2.85	2.80	2.60	2.94	3.22	3.48	3.66	3.62
1202	8	16.22	19.75	3.53	2.30	2.50	2.62	2.75	2.85	2.80	2.60	2.94	3.22	3.48	3.66	3.62
1202	9	16.82	18.21	1.39	2.30	2.50	2.62	2.75	2.85	2.80	2.60	2.94	3.22	3.48	3.66	3.62
2803	7	17.99	19.09	1.10	2.20	2.50	2.60	2.60	2.60	2.60	2.50	2.68	2.82	2.82	2.82	2.78
2803	8	17.91	18.45	.54	2 20	2.50	2.60	2.60	2.60	2.60	2.50	2.68	2.82	2.82	2.82	2.78
2803	9	17.36	18.59	1.23	2.20	2.50	2.60	2.60	2.60	2.60	2.50	2.68	2.82	2.82	2.82	2.78
1604	1	15.07	25.25	10.18	2.10	2.05	2.10	2.15	2.30	2.40	1.76	1.66	1.70	1.82	2.08	2.30
1704	1	14.54	27.25	12.71	2.20	2.10	2.05	2.10	2.15	2.30	1.94	1.76	1.66	1.70	1.82	..08
2304	7	16.59	20.38	3.79	2.70	2.70	2.65	2.60	2.45	2.30	3.00	2.96	2.88	2.68	2.40	2.12
2304	8	16.25	18.95	2.70	2.70	2.70	2.65	2.60	2.45	2.30	3.00	2.96	2.88	2.68	2.40	2.12
2304	9	16.84	19.83	2.99	2.70	2.70	2.65	2.60	2.45	2.30	3.00	2.96	2.88	2.68	2.40	2.12
1005	4	16.92	17.83	.91	2.35	2.40	2.55	2.65	2.70	2.70	2.25	2.42	2.70	2.86	3.00	3.02
1405	7	17.07	24.55	7.48	2.10	2.15	2.20	2.30	2.35	2.40	1.74	1.78	1.90	2.06	2.25	2.42
1405	8	16.42	19.68	3.26	2.10	2.15	2.20	2.30	2.35	2.40	1.74	1.78	1.90	2.06	2.25	2.42
1405	9	12.35	20.29	2.94	2.10	2.15	2.20	2.30	2.35	2.40	1.74	1.78	1.90	2.06	2.25	2.42
2105	1	16.45	22.08	5.63	2.75	2.65	2.55	2.45	2.30	2.20	3.10	2.88	2.72	2.42	2.15	1.90
2105	2	16.07	21.80	5.73	2.75	2.65	2.55	2.45	2.30	2.20	3.10	2.88	2.72	2.42	2.15	1.90
2105	3	16.47	22.20	5.73	2.75	2.65	2.55	2.45	2.30	2.20	3.10	2.88	2.72	2.42	2.15	1.90
2105	4	16.86	19.21	2.35	2.75	2.65	2.55	2.45	2.30	2.20	3.10	2.88	2.72	2.42	2.15	1.90
2105	5	16.78	19.87	3.09	2.75	2.65	2.55	2.45	2.30	2.20	3.10	2.88	2.72	2.42	2.15	1.90
2105	6	16.89	19.41	2.52	2.75	2.65	2.55	2.45	2.30	2.20	3.10	2.88	2.72	2.42	2.15	1.90
2205	1	16.23	18.41	2.18	2.80	2.75	2.65	2.55	2.45	2.30	3.18	3.10	2.88	2.72	2.42	2.15
2905	4	17.78	22.80	5.02	2.50	2.55	2.60	2.70	2.72	2.75	2.50	2.56	2.68	2.86	2.98	3.12
0406	2	16.15	20.30	4.15	2.55	2.55	2.55	2.55	2.40	2.50	2.72	2.72	2.72	2.66	2.55	2.44
0406	3	16.50	20.43	3.93	2.55	2.55	2.55	2.55	2.40	2.50	2.72	2.72	2.72	2.66	2.55	2.44

Table A1 (Continued)

Date	Station	Salinity (o/oo)			High Tide Height (ft.)						Tide Range (ft.)					
		Surface	Bottom	Δ	0	-1	-2	-3	-4	-5	0	-1	-2	-3	-4	-5
0406	4	16.68	18.21	1.53	2.55	2.55	2.55	2.55	2.40	2.50	2.72	2.72	2.72	2.66	2.55	2.44
0406	5	17.72	18.68	.96	2.55	2.55	2.55	2.55	2.40	2.50	2.72	2.72	2.72	2.66	2.55	2.44
0406	6	17.61	18.63	1.02	2.55	2.55	2.55	2.55	2.40	2.50	2.72	2.72	2.72	2.66	2.55	2.44
0406	7	16.49	19.63	3.14	2.55	2.55	2.55	2.55	2.40	2.50	2.72	2.72	2.72	2.66	2.55	2.44
0406	8	17.37	18.24	.87	2.55	2.55	2.55	2.55	2.40	2.50	2.72	2.72	2.72	2.66	2.55	2.44
0406	9	17.67	18.14	.47	2.55	2.55	2.55	2.55	2.40	2.50	2.72	2.72	2.72	2.66	2.55	2.44
1006	4	16.28	19.22	2.94	2.25	2.27	2.35	2.40	2.45	2.50	2.02	2.10	2.30	2.42	2.56	2.64
1806	1	17.37	26.26	8.89	2.65	2.50	2.45	2.30	2.20	2.20	2.88	2.62	2.40	2.08	1.88	1.84
1906	1	17.45	25.55	8.10	2.80	2.65	2.50	2.45	2.30	2.20	3.18	2.88	2.62	2.40	2.08	1.88
1906	2	17.36	25.32	7.96	2.80	2.65	2.50	2.45	2.30	2.20	3.18	2.88	2.62	2.40	2.08	1.88
1906	3	17.26	25.36	8.10	2.80	2.65	2.50	2.45	2.30	2.20	3.18	2.88	2.62	2.40	2.08	1.88
1906	4	17.43	23.83	6.40	2.80	2.65	2.50	2.45	2.30	2.20	3.18	2.88	2.62	2.40	2.08	1.88
1906	5	17.39	25.16	7.77	2.80	2.65	2.50	2.45	2.30	2.20	3.18	2.88	2.62	2.40	2.08	1.88
1906	6	17.24	24.29	7.05	2.80	2.65	2.50	2.45	2.30	2.20	3.18	2.88	2.62	2.40	2.08	1.88
2606	4	18.68	19.69	1.01	2.60	2.70	2.75	2.80	2.90	2.90	2.64	2.86	3.05	3.22	3.40	3.38
0307	2	18.26	23.09	4.83	2.50	2.45	2.45	2.40	2.40	2.40	2.56	2.48	2.42	2.30	2.38	2.28
0307	3	18.12	22.97	4.85	2.50	2.45	2.45	2.40	2.40	2.40	2.56	2.48	2.42	2.30	2.28	2.28
0307	4	17.78	21.67	3.89	2.50	2.45	2.45	2.40	2.40	2.40	2.56	2.48	2.42	2.30	2.28	2.28
0307	5	17.89	22.77	4.88	2.50	2.45	2.45	2.40	2.40	2.40	2.56	2.48	2.42	2.30	2.28	2.28
0307	6	17.77	22.08	4.31	2.50	2.45	2.45	2.40	2.40	2.40	2.56	2.48	2.42	2.30	2.28	2.28
1007	4	18.33	22.39	4.06	2.35	2.35	2.35	2.40	2.45	2.50	2.06	2.12	2.24	2.36	2.46	2.50
1107	7	20.14	24.58	4.44	2.30	2.35	2.35	2.35	2.40	2.45	1.98	2.06	2.12	2.24	2.36	2.46
1107	8	19.68	21.14	1.46	2.30	2.35	2.35	2.35	2.40	2.45	1.98	2.06	2.12	2.24	2.36	2.46
1107	9	19.22	21.83	2.61	2.30	2.35	2.35	2.35	2.40	2.45	1.98	2.06	2.12	2.24	2.36	2.46
1807	2	17.50	25.20	7.70	2.85	2.70	2.60	2.45	2.35	2.25	3.16	2.88	2.60	2.26	2.06	1.88
1807	3	17.91	25.32	7.41	2.85	2.70	2.60	2.45	2.35	2.25	3.16	2.88	2.60	2.26	2.06	1.88
1807	4	18.38	23.54	5.16	2.85	2.70	2.60	2.45	2.35	2.25	3.16	2.88	2.60	2.26	2.06	1.88

Table A1 (Continued)

Date	Station	Salinity (o/oo) Surface	Bottom	Δ	High Tide Height (ft.) 0	-1	-2	-3	-4	-5	Tide Range (ft.) 0	-1	-2	-3	-4	-5
1807	5	18.49	23.47	4.48	2.85	2.70	2.60	2.45	2.35	2.25	3.16	2.88	2.60	2.26	2.06	1.88
1807	6	18.68	24.42	5.74	2.85	2.70	2.60	2.45	2.35	2.25	3.16	2.88	2.60	2.26	2.06	1.88
2207	7	20.27	20.41	.14	3.00	3.05	3.05	3.00	2.85	2.70	3.42	3.54	3.56	3.40	3.16	2.88
2207	8	20.47	20.45	.01	3.00	3.05	3.05	3.00	2.85	2.70	3.42	3.54	3.56	3.40	3.16	2.88
2307	1	20.41	20.59	.18	3.00	3.00	3.05	3.05	3.00	2.85	3.22	3.42	3.54	3.56	3.40	3.16
2407	1	20.25	20.39	.14	2.85	3.00	3.00	3.05	3.05	3.00	2.94	3.22	3.42	3.54	3.56	3.40
2507	4	20.41	20.45	.04	2.70	2.85	3.00	3.00	3.05	3.05	2.58	2.94	3.22	3.42	3.54	3.56
0108	7	19.18	21.82	2.64	2.55	2.55	2.40	2.40	2.40	2.40	2.40	2.26	2.16	2.07	2.02	2.04
0108	8	19.68	21.02	1.34	2.55	2.55	2.40	2.40	2.40	2.40	..40	2.26	2.16	2.07	2.02	2.04
0108	9	19.56	11.01	1.45	2.55	2.55	2.40	2.40	2.40	2.40	2.40	2.26	2.16	2.07	2.02	2.04
0208	2	18.50	24.03	5.53	2.60	2.55	2.55	2.40	2.40	2.40	2.50	2.40	2.26	2.16	2.07	2.02
0208	3	19.01	23.90	4.89	2.60	2.55	2.55	2.40	2.40	2.40	2.50	2.40	2.26	2.16	2.07	.02
0208	4	19.85	23.48	3.63	2.60	2.55	2.55	2.40	2.40	2.40	2.50	2.40	2.26	2.16	2.07	2.02
0208	5	19.81	23.30	3.51	2.60	2.55	2.55	2.40	2.40	2.40	2.50	2.40	2.26	2.16	2.07	2.02
0208	6	19.35	22.52	3.17	2.60	2.55	2.55	2.40	2.40	2.40	2.50	2.40	2.26	2.16	2.07	2.02
0908	4	20.00	21.13	1.13	2.45	2.47	2.50	2.55	2.60	2.60	2.00	2.17	2.26	2.38	2.48	2.50
0908	7	20.54	21.48	.94	2.55	2.47	2.50	2.55	2.60	2.60	2.00	2.17	2.26	2.38	2.48	2.50
0908	8	20.21	21.10	.89	2.45	2.47	2.50	2.5	2.60	2.60	2.00	2.17	2.26	2.38	2.48	2.50
0908	9	19.67	21.04	1.37	2.45	2.47	2.50	2.55	2.60	2.60	2.00	2.17	2.26	2.38	2.48	2.50
1608	2	19.38	24.08	4.70	3.05	2.85	2.65	2.55	2.45	2.40	3.26	2.90	2.50	2.20	1.98	1.92
1608	3	19.94	24.16	4.22	3.05	2.85	2.65	2.55	2.45	2.40	3.26	2.90	2.50	2.20	1.98	1.92
1608	4	19.82	22.74	2.92	3.05	2.85	2.65	2.55	2.45	2.40	3.26	2.90	2.50	2.20	1.98	1.92
1608	5	19.64	22.96	3.32	3.05	2.85	2.65	2.55	2.45	2.40	3.26	2.90	2.50	2.20	1.98	1.92
1608	6	19.71	22.89	2.18	3.05	2.85	2.65	2.55	2.45	2.40	3.26	2.90	2.50	2.20	1.98	1.92
2108	1	20.53	20.60	.07	3.05	3.15	3.25	3.25	3.15	3.05	3.25	3.46	.62	3.66	3.50	3.26
2208	1	20.53	20.56	.03	2.95	3.05	3.15	3.25	3.25	3.15	2.84	3.25	3.46	3.62	3.66	3.50
2308	4	19.95	20.15	.70	2.80	2.95	3.05	3.15	3.25	3.25	2.48	2.84	3.25	3.46	3.62	3.66

Table A1 (Continued)

Date	Station	Salinity (o/oo)			High Tide Height (ft.)						Tide Range (ft.)					
		Surface	Bottom	Δ	0	-1	-2	-3	-4	-5	0	-1	-2	-3	-4	-5
3008	2	19.90	23.84	3.94	2.65	2.55	2.45	2.45	2.40	2.45	2.32	2.20	1.97	1.88	1.80	1.88
3008	3	19.77	23.66	3.89	2.65	2.55	2.45	2.45	2.40	2.45	2.32	2.20	1.97	1.88	1.80	1.88
3008	4	19.83	23.82	3.99	2.65	2.55	2.45	2.45	2.40	2.45	2.32	2.20	1.97	1.88	1.80	1.88
3008	5	19.78	23.89	4.11	2.65	2.55	2.45	2.45	2.40	2.45	2.32	2.20	1.97	1.88	1.80	1.88
3008	6	19.66	23.49	3.83	2.65	2.55	2.45	2.45	2.40	2.45	2.32	2.20	1.97	1.88	1.80	1.88
0309	7	21.53	23.65	2.12	2.80	2.80	2.75	2.70	2.65	2.55	2.60	2.62	2.52	2.44	2.32	2.20
0309	8	21.35	21.90	.55	2.80	2.80	2.75	2.70	2.65	2.55	2.60	2.62	2.52	2.44	2.32	2.20
0309	9	21.81	22.87	1.06	2.80	2.80	2.75	2.70	2.65	2.55	2.60	2.62	2.52	2.44	2.32	2.20
1009	4	17.21	21.39	4.18	2.55	2.55	2.60	2.60	2.65	2.70	2.02	1.96	2.08	2.12	2.28	2.40
1609	2	19.67	21.37	1.70	3.35	3.25	3.15	2.95	2.75	2.60	3.62	3.46	3.22	2.88	2.50	2.16
1609	3	19.34	21.17	1.83	3.35	3.25	3.15	2.95	2.75	2.60	3.62	3.46	3.22	2.88	2.50	2.16
1609	4	18.84	21.36	2.52	3.35	3.25	3.15	2.95	2.75	2.60	3.62	3.46	3.22	2.88	2.50	2.16
1609	5	18.68	21.46	2.78	3.35	3.25	3.15	2.95	2.75	2.60	3.62	3.46	3.22	2.88	2.50	2.16
1609	6	17.95	20.90	2.55	3.35	3.25	3.15	2.95	2.75	2.60	3.62	3.46	3.22	2.88	2.50	2.16
2309	4	18.36	23.19	4.83	2.50	2.60	2.75	2.90	3.05	3.20	1.80	2.04	2.34	2.75	3.02	3.32
0110	1	20.29	23.85	3.56	2.85	2.85	2.80	2.65	2.60	2.45	2.66	2.60	2.50	2.28	2.12	1.86
0210	1	20.58	23.36	2.78	2.90	2.85	2.85	2.80	2.65	2.60	2.72	2.66	2.60	2.50	2.28	2.12
0210	4	19.90	24.24	4.34	2.90	2.85	2.85	2.80	2.65	2.60	2.72	2.66	2.60	2.50	2.28	2.12
0710	7	20.77	21.59	.82	2.65	2.70	2.75	2.80	2.85	2.90	2.18	2.40	2.42	2.56	2.68	2.72
0710	8	21.96	21.38	.01	2.65	2.70	2-75	2.80	2.85	2.90	2.18	2.40	2.42	2.56	2.68	2.72
0710	9	20.31	21.30	.99	2.65	2.70	2.75	2.80	2.85	2.90	2.18	2.40	2.42	2.56	2.68	2.72
1010	4	20.53	22.71	2.18	2.65	2.55	2.55	2.65	2.70	2.75	2.30	2.12	2.04	2.18	2.40	2.42
0711	7	22.28	23.72	1.44	2.50	2.50	2.55	2.65	2.75	2.75	2.30	2.28	2.36	2.62	2.64	2.74
0711	8	22.01	22.52	.51	2.50	2.50	2.55	2.65	2.75	2.75	2.30	2.28	2.36	2.62	2.64	2.74
0711	9	22.14	22.81	.67	2.50	2.50	2.55	2.65	2.75	2.75	2.30	2.28	2.36	2.62	2.64	2.74

Table A1 (Continued)

Date	Station	Salinity (o/oo)			High Tide Height (ft.)						Tide Range (ft.)					
		Surface	Bottom	Δ	0	-1	-2	-3	-4	-5	0	-1	-2	-3	-4	-5
1311	1	22.59	23.67	1.06	2.85	2.85	2.75	2.70	2.60	2.50	3.04	3.00	2.82	2.72	2.60	2.38
1411	1	22.45	24.64	2.19	2.85	2.85	2.85	2.75	2.70	2.60	3.02	3.04	3.00	2.82	2.72	2.60
0512	7	23.43	25.35	1.92	2.45	2.55	2.62	2.70	2.70	2.70	2.60	2.74	2.95	2.96	2.98	2.98
0512	8	18.07	19.83	1.76	2.45	2.55	2.62	2.70	2.70	2.70	2.60	2.74	2.95	2.96	2.98	2.98
0512	9	23.83	26.38	2.55	2.45	2.55	2.62	2.70	2.70	2.70	2.60	2.74	2.95	2.96	2.98	2.98

Table A2. Salinity and tide data from the lower Rappahannock River for 1974. Date, station, surface and bottom salinities, surface-to-bottom salinity differences (Δ), mean daily predicted high tide height (H), and mean daily predicted tide range (R) are shown. Values of both H and R are shown for the same day as the salinity observation (0), and for the five days prior to that (-1,-2.... -5). Values of both H and R are given in feet for Hampton Roads, Virginia. To convert to meters for the lower Rappahannock River divide by 0.6096. Station locations are: Norris Bridge, 37°37'07"N. latitude, 76°25'45"W. longitude; Smoky Point 37°43'14"N. latitude, 76°34'53"W. longitude.

Date	Salinity (o/oo)						High Tide Height (ft.)						Tide Range (ft.)					
	Norris Bridge			Smoky Point														
	Surface	Bottom	Δ	Surface	Bottom	Δ	0	-1	-2	-3	-4	-5	0	-1	-2	-3	-4	-5
1806	12.0	15.2	3.20				2.65	2.50	2.45	2.30	2.20	2.20	2.88	2.62	2.40	2.08	1.88	1.84
1906	12.2	15.0	2.80				2.80	2.65	2.50	2.45	2.30	2.20	3.18	2.88	2.62	2.40	2.08	1.88
2006	12.4	14.8	2.40				2.85	2.80	2.65	2.50	2.45	2.30	3.32	3.18	2.88	2.62	2.40	2.08
2106	12.8	14.7	1.90				2.90	2.85	2.80	2.65	2.50	2.45	3.38	3.32	3.18	2.88	2.62	2.40
2206	13.1	15.9	2.80				2.90	2.90	2.85	2.80	2.65	2.50	3.40	3.38	3.32	3.18	2.88	2.62
2306	13.1	15.8	2.70				2.80	2.90	2.90	2.85	2.80	2.65	3.22	3.40	3.38	3.32	3.18	2.88
2406	13.0	14.9	1.90				2.75	2.80	2.90	2.90	2.85	2.80	3.05	3.22	3.40	3.38	3.32	3.18
2506	13.2	13.4	0.20				2.70	2.75	2.80	2.90	2.90	2.85	2.86	3.05	3.22	3.40	3.38	3.32
2606	13.7	13.9	0.20				2.60	2.70	2.75	2.80	2.90	2.90	2.64	2.86	3.05	3.22	3.40	3.38
2706	13.9	14.3	0.40				2.50	2.60	2.70	2.75	2.80	2.90	2.42	2.64	2.86	3.05	3.22	3.40
2806	14.0	14.4	0.40				2.40	2.50	2.60	2.70	2.75	2.80	2.28	2.42	2.64	2.86	3.05	3.22
2906	13.4	13.9	0.50				2.40	2.40	2.50	2.60	2.70	2.75	2.28	2.28	2.42	2.64	2.86	3.05
3006	13.2	13.7	0.50				2.40	2.40	2.40	2.50	2.60	2.70	2.30	2.28	2.28	2.42	2.64	2.86
0107	13.2	13.8	0.60				2.45	2.40	2.40	2.40	2.50	2.60	2.42	2.30	2.28	2.28	2.42	2.64
0207	13.5	14.9	1.40				2.45	2.45	2.40	2.40	2.40	2.50	2.48	2.42	2.30	2.28	2.28	2.42
0307	13.1	14.6	1.50				2.50	2.45	2.45	2.40	2.40	2.40	2.56	2.48	2.42	2.30	2.28	2.28
0407	13.0	14.5	1.50				2.45	2.50	2.45	2.45	2.40	2.40	2.48	2.56	2.48	2.42	2.30	2.28
0507	13.4	14.3	0.90				2.50	2.45	2.50	2.45	2.45	2.40	2.50	2.48	2.56	2.48	2.42	2.30
0607	13.6	14.8	1.20				2.45	2.50	2.45	2.50	2.45	2.45	2.46	2.50	2.48	2.56	2.48	2.42
0707	13.8	15.5	1.70				2.40	2.45	2.50	2.45	2.50	2.45	2.36	2.46	2.50	2.48	2.56	2.48

Table A2 (Continued)

Date	Salinity (o/oo)						High Tide Height (ft.)						Tide Range (ft.)					
	Norris Bridge			Smoky Point														
	Surface	Bottom	Δ	Surface	Bottom	Δ	0	-1	-2	-3	-4	-5	0	-1	-2	-3	-4	-5
0807	13.4	15.7	2.30				2.35	2.40	2.45	2.50	2.45	2.50	2.24	2.36	2.46	2.50	2.48	2.56
0907	13.4	16.1	2.70				2.35	2.35	2.40	2.45	2.50	2.45	2.12	2.24	2.36	2.46	2.50	2.48
1007	13.4	15.9	2.50				2.35	2.35	2.35	2.40	2.45	2.50	2.06	2.12	2.24	2.36	2.46	2.50
1107	12.9	15.6	3.30				2.30	2.35	2.35	2.35	2.40	2.45	1.98	2.06	2.12	2.24	2.36	2.46
1207	13.0	15.1	2.10				2.30	2.30	2.35	2.35	2.35	2.40	1.92	1.98	2.06	2.12	2.24	2.36
1307	13.0	14.9	1.90				2.25	2.30	2.30	2.35	2.35	2.35	1.88	1.92	1.98	2.06	2.12	2.24
1407	13.2	14.5	1.30				2.35	2.25	2.30	2.30	2.35	2.35	2.06	1.88	1.92	1.98	2.06	2.12
1507	13.2	14.2	1.00				2.45	2.35	2.25	2.30	2.30	2.35	2.26	2.06	1.88	1.92	1.98	2.06
1607	13.3	14.2	0.90				2.60	2.45	2.35	2.25	2.30	2.30	2.60	2.26	2.06	1.88	1.92	1.98
1707	13.5	14.2	0.70				2.70	2.60	2.45	2.35	2.25	2.30	2.88	2.60	2.26	2.06	1.88	1.92
1807	13.7	14.1	0.40				2.85	2.70	2.60	2.45	2.35	2.25	3.16	2.88	2.60	2.26	2.06	1.88
1907	13.8	14.2	0.40	13.2	13.2	0.01	3.00	2.85	2.70	2.60	2.45	2.35	3.40	3.16	2.88	2.60	2.26	2.06
2007	13.8	14.1	0.30	13.2	13.2	0.01	3.05	3.00	2.85	2.70	2.60	2.45	3.56	3.40	3.16	2.88	2.60	2.26
2107	14.0	14.5	0.50	13.3	13.5	0.20	3.05	3.05	3.00	2.85	2.70	2.60	3.54	3.56	3.40	3.16	2.88	2.60
2207	14.2	14.5	0.30	13.5	13.6	0.10	3.00	3.05	3.05	3.00	2.85	2.70	3.42	3.54	3.56	3.40	3.16	2.88
2307	14.4	14.8	0.40	13.5	13.5	0.01	3.00	3.00	3.05	3.05	3.00	2.85	3.22	3.42	3.54	3.56	3.40	3.16
2407	14.5	14.8	0.30	13.6	13.6	0.01	2.85	3.00	3.00	3.05	3.05	3.00	2.94	3.22	3.42	3.54	3.56	3.40
2507	14.5	14.8	0.30	13.6	13.5	0.01	2.70	2.85	3.00	3.00	3.05	3.05	2.58	2.94	3.22	3.42	3.54	3.56
2607	14.5	15.0	0.50	13.6	13.5	0.01	2.55	2.70	2.85	3.00	3.00	3.05	2.30	2.58	2.94	3.22	3.42	3.54
2707	14.4	14.8	0.40	13.3	13.4	0.10	2.40	2.55	2.70	2.85	3.00	3.00	2.04	2.30	2.58	2.94	3.22	3.42
2807	14.3	14.8	0.50	13.1	13.5	0.40	2.40	2.40	2.55	2.70	2.85	3.00	2.02	2.04	2.30	2.58	2.94	3.22
2907	14.4	14.7	0.30	13.1	13.5	0.40	2.40	2.40	2.40	2.55	2.70	2.85	2.07	2.02	2.04	2.30	2.58	2.94
3007	14.5	14.8	0.30	13.2	13.4	0.40	2.40	2.40	2.40	2.40	2.55	2.70	2.16	2.07	2.02	2.04	2.30	2.58
3107	14.3	14.7	0.40	13.0	13.8	0.80	2.55	2.40	2.40	2.40	2.40	2.55	2.26	2.16	2.07	2.02	2.04	2.30
0108	14.3	14.9	0.60	12.9	14.1	1.20	2.55	2.55	2.40	2.40	2.40	2.40	2.40	2.26	2.16	2.07	2.02	2.04
0208	14.4	14.8	0.40	13.2	13.9	0.70	2.60	2.55	2.55	2.40	2.40	2.40	2.50	2.40	2.26	2.16	2.07	2.02
0308	14.5	15.3	0.80	13.2	13.3	0.10	2.65	2.60	2.55	2.55	2.40	2.40	2.54	2.50	2.40	2.26	2.16	2.07

Table A2 (Continued)

Date	Salinity (o/oo)						High Tide Height (ft.)						Tide Range (ft.)					
	Norris Bridge			Smoky Point														
	Surface	Bottom	Δ	Surface	Bottom	Δ	0	-1	-2	-3	-4	-5	0	-1	-2	-3	-4	-5
0408	14.6	16.2	1.60	13.1	13.3	0.20	2.60	2.65	2.60	2.55	2.55	2.40	2.50	2.54	2.50	2.40	2.26	2.16
0508	14.6	17.1	2.50	13.0	14.7	1.70	2.60	2.60	2.65	2.60	2.55	2.55	2.48	2.50	2.54	2.50	2.40	2.26
0608	15.8	17.9	2.10	13.1	16.7	3.60	2.55	2.60	2.60	2.65	2.60	2.55	2.38	2.48	2.50	2.54	2.50	2.40
0708	15.8	17.3	1.50	13.3	15.9	2.60	2.50	2.55	2.60	2.60	2.65	2.60	2.26	2.38	2.48	2.50	2.54	2.50
0808	15.1	17.0	1.90	13.1	15.8	2.70	2.50	2.50	2.55	2.60	2.60	2.65	2.17	2.26	2.38	2.48	2.50	2.54
0908	15.4	17.0	1.60	13.0	16.4	3.40	2.45	2.50	2.50	2.55	2.60	2.60	2.00	2.17	2.26	2.38	2.45	2.50
1008	15.3	16.7	1.40	13.1	16.7	3.60	2.45	2.45	2.50	2.50	2.55	2.60	2.00	2.00	2.17	2.26	2.38	2.48
1108				14.1	16.6	2.50	2.40	2.45	2.45	2.50	2.50	2.55	1.92	2.00	2.00	2.17	2.26	2.38
1208				13.3	16.3	3.00	2.45	2.40	2.45	2.45	2.50	2.50	1.98	1.92	2.00	2.00	2.17	2.26
1308				13.1	16.2	3.10	2.55	2.45	2.40	2.45	2.45	2.50	2.20	1.98	1.92	2.00	2.00	2.17
1408				13.4	16.3	2.90	2.65	2.55	2.45	2.40	2.45	2.45	2.50	2.20	1.98	1.92	2.00	2.00
1508				13.1	16.3	3.20	2.85	2.65	2.55	2.45	2.40	2.45	2.90	2.50	2.20	1.98	1.92	2.00
1608				13.5	15.7	2.20	3.05	2.85	2.65	2.55	2.45	2.40	3.26	2.90	2.50	2.20	1.98	1.92
1708				13.8	14.6	0,80	3.15	3.05	2.85	2.65	2.55	2.45	3.50	3.26	2.90	2.50	2.20	1.98
1808				13.8	14.4	0.60	3.25	3.15	3.05	2.85	2.65	2.55	3.66	3.50	3.26	2.90	2.50	2.20
1908	15.3	15.4	0.10	13.1	13.5	0.40	3.25	3.25	3.15	3.05	2.85	2.65	3.62	3.66	3.50	3.26	2.90	2.50
2008	15.4	15.5	0.10	14.1	14.4	0.30	3.15	3.25	3.25	3.15	3.05	2.85	3.46	3.62	3.66	3.50	3.26	2.90
2108	15.5	15.4	0.01	14.2	14.3	0.10	3.05	3.15	3.25	3.25	3.15	3.05	3.25	3.46	3.62	3.66	3.50	3.26
2208	15.5	15.4	0.01	8.9	8.8	0.01	2.95	3.05	3.15	3.25	3.25	3.15	2.84	3.25	3.46	3.62	3.66	3.50
2308	15.3	15.4	0.10	11.0	10.8	0.01	2.80	2.95	3.05	3.15	3.25	3.25	2.48	2.84	3.25	3.46	3.62	3.66
2408	15.0	15.2	0.20	13.8	13.7	0.01	2.60	2.80	2.95	3.05	3.15	3.25	2.12	2.48	2.84	3.25	3.46	3.62
2508	15.0	15.2	0.20	13.7	13.6	0.01	2.45	2.60	2.80	2.95	3.05	3.15	1.88	2.12	2.48	2.84	3.25	3.46
2608	15.3	15.7	0.40	13.5	13.7	0.20	2.40	2.45	2.60	2.80	2.95	3.05	1.80	1.88	2.12	2.48	2.84	3.25
2708	15.4	15.7	0.30	13.9	14.5	0.60	2.40	2.40	2.45	2.60	2.80	2.95	1.88	1.80	1.88	2.12	2.48	2.84
2808	15.3	15.9	0.60	13.2	13.6	0.40	2.45	2.40	2.40	2.45	2.60	2.80	1.97	1.88	1.80	1.88	2.12	2.48
2908	15.4	16.5	1.10	13.3	14.9	1.60	2.55	2.45	2.40	2.40	2.45	2.60	2.20	1.97	1.88	1.80	1.88	2.12

Table A2 (Continued)

Date	Salinity (o/oo)						High Tide Height (ft.)						Tide Range (ft.)					
	Norris Bridge			Smoky Point														
	Surface	Bottom	Δ	Surface	Bottom	Δ	0	-1	-2	-3	-4	-5	0	-1	-2	-3	-4	-5
3008	15.5	17.5	2.00	12.9	16.8	2.90	2.65	2.55	2.45	2.45	2.40	2.45	2.32	2.20	1.97	1.88	1.80	1.88
3108	15.4	18.1	2.70	13.0	18.3	5.30	2.70	2.65	2.55	2.45	2.45	2.40	2.42	2.32	2.20	1.97	1.88	1.80
0109	15.8	18.3	2.50	13.2	18.0	4.80	2.75	2.70	2.65	2.55	2.45	2.45	2.52	2.42	2.32	2.20	1.97	1.88
0209	15.7	18.3	2.60	13.5	18.0	4.50	2.80	2.75	2.70	2.65	2.55	2.45	2.62	2.52	2.42	2.32	2.20	1.97
0309	16.4	17.7	1.30	13.8	16.7	2.90	2.80	2.80	2.75	2.70	2.65	2.55	2.60	2.62	2.52	2.42	2.32	2.20
0409	16.3	17.2	0.90	14.3	17.6	3.30	2.75	2.80	2.80	2.75	2.70	2.65	2.50	2.60	2.62	2.52	2.42	2.32
0509	16.5	16.8	0.30	14.5	17.5	3.00	2.70	2.75	2.80	2.80	2.75	2.70	2.40	2.50	2.60	2.62	2.52	2.42
0609	16.6	16.7	0.10	15.0	17.1	2.10	2.65	2.70	2.75	2.80	2.80	2.75	2.28	2.40	2.50	2.60	2.62	2.52
0709	16.4	16.5	0.10	14.8	16.1	1.30	2.62	2.65	2.70	2.75	2.80	2.80	2.12	2.28	2.40	2.50	2.60	2.62
0809	15.7	16.1	0.40	14.2	16.2	2.00	2.60	2.62	2.65	2.70	2.75	2.80	2.08	2.12	2.28	2.40	2.50	2.60
0909	15.9	16.4	0.50	13.6	15.9	2.30	2.55	2.60	2.62	2.65	2.70	2.75	1.86	2.08	2.12	2.28	2.40	2.50

APPENDIX B

Environmental and primary productivity data for the lower York River for 1974.

Table B1. Primary productivity data for the lower York River for 1974. Date, time and depth of sample collection are shown. Rates of primary productivity, chlorophyll content and assimilation ratios are given for both the total phytoplankton and the nannoplankton. The mean incubation light intensity (langleys per minute) and the midtime of the incubations are also shown. Incubations normally lasted for two hours.

			TOTAL PHYTOPLANKTON			NANNOPLANKTON				
DATE	TIME EST	DEPTH m	PRIM PROD µgC/l/hr	CHL a µg/l	ASSIM RATIO µgC/hr/µg Chl a	PRIM PROD µgC/l/hr	CHL a µg/l	ASSIM RATIO µgC/hr/µg Chl a	INC LIGHT L/min	INC TIME EST
11 II 74	0600	0.5	19.5	7.99	2.10	4.08	3.64	.96	.144	0810
		1.0	19.01	5.07	3.20	3.79	2.87	1.13	.104	
		2.0	8.80	4.97	1.51	2.78	2.77	.85	.054	
		4.0	.79	2.31	.29	.17	3.84	.04	.014	
	0800	0.5								
		1.0	All samples lost.							
		2.0								
		4.0								
	1000	0.5	75.98	4.86	19.84	5.08	3.81	1.69	.447	1145
		1.0	52.29	7.34	9.04	2.73	4.09	.85	.323	
		2.0	34.06	8.64	5.00	3.91	3.79	1.31	.174	
		4.0	14.03	5.72	3.11	1.71	3.61	.60	.056	
	1200	0.5	36.49	5.29	6.65	7.50	3.42	2.11	.519	1345
		1.0	33.76	5.62	5.79	5.19	3.33	1.50	.368	
		2.0	28.46	5.51	4.98	4.80	3.54	1.30	.187	
		4.0	15.94	7.02	2.19	2.52	4.22	.58	.043	

Table B1 (Continued).

DATE	TIME EST	DEPTH m	TOTAL PHYTOPLANKTON PRIM PROD µgC/l/hr	CHL a µg/l	ASSIM RATIO µgC/hr/µg Chl a	NANNOPLANKTON PRIM PROD µgC/l/hr	CHL a µg/l	ASSIM RATIO µgC/hr/µgChl a	INC LIGHT L/min	INC TIME EST
	1400	0.5	24.3	5.51	4.11	4.2	3.61	1.08	.316	1535
		1.0	26.89	7.67	3.26	3.74	3.50	.99	.220	
		2.0	17.56	10.66	1.53	4.78	3.21	1.38	.105	
		4.0	1.14	8.21	.129	.207	2.66	.07	.027	
	1600	0.5	4.49	8.96	.538	2.49	2.91	.92	.033	1730
		1.0	7.34	6.05	1.30	1.06	3.04	.37	.022	
		2.0	3.65	7.99	.491	.65	3.04	.23	.009	
		4.0	-	5.98	-	-	2.87	-	.002	

Table B1 (Continued).

DATE	TIME EST	DEPTH m	TOTAL PHYTOPLANKTON PRIM PROD µgC/l/hr	CHL a µg/l	ASSIM RATIO µgC/hr/µg Chl a	NANNOPLANKTON PRIM PROD µgC/l/hr	CHL a µg/l	ASSIM RATIO µgC/hr/µg Chl a	INC LIGHT L/min	INC TIME EST
16 IV 74	0500	0.5	4.46	7.43	.60	4.49	5.57	.80	.149	0650
		1.0	3.78	7.60	.49	3.75	4.98	.75	.103	
		2.0	3.67	7.17	.51	2.06	5.36	.38	.055	
		4.0	.95	7.26	.13	1.17	5.19	.22	.015	
	0700	0.5	7.72	6.03	1.28	4.91	5.11	.96	.487	0845
		1.0	8.82	8.27	1.06	6.73	5.11	1.31	.341	
		2.0	7.35	7.60	.97	6.18	5.32	1.16	.144	
		4.0	3.73	8.19	.45	1.70	5.65	.30	.039	
	0900	0.5	8.86	7.43	1.19	7.07	4.43	1.59	.590	1045
		1.0	8.51	6.41	1.33	7.40	4.01	1.84	.433	
		2.0	7.13	8.02	.89	6.67	4.64	1.44	.207	
		4.0	3.63	9.54	.38	2.71	7.34	.37	.038	
	1100	0.5	11.43	7.93	1.44	7.42	5.74	1.29	.653	1245
		1.0	14.56	7.60	1.91	8.45	6.16	1.37	.443	
		2.0	14.39	9.20	1.56	9.56	7.60	1.25	.197	
		4.0	66.14	17.22	.35	3.17	9.45	.33	.032	
	1300	0.5	21.92	10.47	2.09	19.32	7.17	2.69	.498	1420
		1.0	27.35	13.00	2.10	21.27	10.46	2.03	.352	
		2.0	23.10	17.22	1.34	15.28	10.80	1.42	.137	
		4.0	6.18	17.22	.36	3.52	9.96	.35	.019	
	1500	0.5	8.94	7.85	1.14	7.70	3.71	2.07	.372	1625
		1.0	13.13	8.36	1.57	9.82	5.23	1.87	.257	
		2.0	6.02	9.62	.62	4.97	5.15	.96	.095	
		4.0	2.42	15.95	.15	1.18	7.09	.16	.019	

Table B1 (Continued).

DATE	TIME	DEPTH	TOTAL PHYTOPLANKTON PRIM PROD	CHL a	ASSIM RATIO	NANNOPLANKTON PRIM PROD	CHL a	ASSIM RATIO	INC LIGHT	INC TIME
	EST	m	µgC/l/hr	µg/l	µgC/hr/µg Chl a	µgC/l/hr	µg/l	µgC/hr/µg Chl a	L/min	EST
	1700	0.5	4.32	8.86	.48	2.96	4.81	.61	.101	1755
		1.0	2.33	9.96	.23	1.57	5.82	.27	.069	
		2.0	1.76	9.12	.19	-	5.23	-	.027	
		4.0	1.44	15.70	.09	.08	6.50	.01	.006	

Table B1 (Continued).

DATE	TIME EST	DEPTH m	TOTAL PHYTOPLANKTON PRIM PROD µgC/l/hr	CHL a µg/l	ASSIM RATIO µgC/hr/µg Chl a	NANNOPLANKTON PRIM PROD µgC/l/hr	CHL a µg/l	ASSIM RATIO µgC/hr/µg Chl a	INC LIGHT L/min	INC TIME EST
21 V 74	0500	0.5	14.32	9.28	1.54	7.20	4.52	1.59	.140	0640
		1.0	12.03	10.38	1.16	3.64	3.80	.96	.098	
		2.0	6.78	10.80	.63	2.43	3.12	.78	.038	
		4.0	.34	10.47	.03	2.28	3.33	.68	.007	
	0700	0.5	24.12	13.80	1.75	5.93	4.98	1.19	.420	0845
		1.0	22.99	11.27	2.04	7.71	4.18	1.84	.320	
		2.0	20.11	11.14	1.80	5.84	4.77	1.22	.130	
		4.0	10.72	11.27	.95	4.60	4.56	1.07	.025	
	0900	0.5	24.29	11.48	2.12	9.42	4.43	2.14	.650	1050
		1.0	19.66	12.15	1.62	6.82	4.35	1.57	.510	
		2.0	11.22	13.25	1.20	2.90	4.64	.62	.270	
		4.0	7.81	12.15	.64	4.03	5.06	.80	.051	
	1100	0.5	19.28	12.53	1.54	8.59	6.54	1.31	.550	1235
		1.0	29.70	11.27	2.38	9.70	5.91	1.64	.440	
		2.0	20.11	12.66	1.59	9.36	5.28	1.77	.250	
		4.0	10.16	14.18	.72	4.59	7.51	.61	.044	
	1300	0.5	17.38	11.39	1.52	2.22	4.52	.49	.580	1430
		1.0	21.68	12.15	1.78	9.25	4.81	1.92	.430	
		2.0	13.55	7.43	1.82	7.02	5.32	1.32	.210	
		4.0	10.27	11.39	.90	2.10	4.60	.46	.042	
	1500	0.5	23.85	13.67	1.74	8.79	6.16	1.43	.340	1630
		1.0	14.84	11.77	1.26	7.50	5.36	1.40	.210	
		2.0	16.01	11.14	1.44	7.15	5.53	1.29	.090	
		4.0	6.32	12.41	.51	2.60	7.60	.34	.018	

Table B1 (Continued).

DATE	TIME EST	DEPTH m	TOTAL PHYTOPLANKTON PRIM PROD µgC/l/hr	TOTAL PHYTOPLANKTON CHL a µg/l	TOTAL PHYTOPLANKTON ASSIM RATIO µgC/hr/µg Chl a	NANNOPLANKTON PRIM PROD µgC/l/hr	NANNOPLANKTON CHL a µg/l	NANNOPLANKTON ASSIM RATIO µgC/hr/µg Chl a	INC LIGHT L/min	INC TIME EST
18 VI 74	0400	0.5	15.29	8.27	1.84	9.65	4.52	2.13	.176	0610
		1.0	9.11	9.96	.91	15.80	5.78	2.73	.119	
		2.0	6.67	9.62	.69	4.61	5.65	.82	.039	
		4.0	-	9.28	-	-	5.36	-	.008	
	0600	0.5	33.24	6.16	5.39	18.79	4.47	4.20	.324	0740
		1.0	31.15	7.09	4.39	22.84	4.77	4.78	.229	
		2.0	16.59	5.99	2.77	12.97	4.68	2.77	.094	
		4.0	5.89	7.60	-	3.19	4.19	.77	.017	
	0800	0.5	27.62	6.58	4.19	25.39	5.74	4.42	.424	0925
		1.0	40.83	8.02	5.09	28.80	6.41	4.49	.323	
		2.0	27.48	8.61	3.19	15.95	5.91	2.69	.156	
		4.0	10.98	8.69	1.26	5.75	7.51	.76	.027	
	1000	0.5	47.79	7.85	6.08	25.49	5.91	4.31	.582	1140
		1.0	47.31	8.27	5.72	22.71	6.67	3.40	.423	
		2.0	34.03	9.71	3.50	24.28	6.33	3.83	.198	
		4.0	15.11	9.54	1.58	5.31	7.34	.72	.033	
	1200	0.5	45.71	8.44	5.41	41.33	6.03	6.85	.578	1335
		1.0	42.40	11.39	3.72	33.09	6.08	5.44	.385	
		2.0	29.18	10.55	2.76	12.78	5.65	2.26	.141	
		4.0	3.94	10.13	.38	.93	6.20	.15	.021	
	1400	0.5	54.17	12.49	4.33	50.68	12.41	4.08	.320	1530
		1.0	54.47	11.65	4.67	35.47	13.08	2.71	.179	
		2.0	20.38	12.91	1.57	13.85	11.65	1.18	.052	
		4.0	3.76	15.57	.24	3.18	9.45	.52	.006	

Table B1 (Continued).

DATE	TIME	DEPTH	TOTAL PHYTOPLANKTON PRIM PROD	TOTAL PHYTOPLANKTON CHL a	TOTAL PHYTOPLANKTON ASSIM RATIO	NANNOPLANKTON PRIM PROD	NANNOPLANKTON CHL a	NANNOPLANKTON ASSIM RATIO	INC LIGHT	INC TIME
	EST	m	µgC/l/hr	µg/l	µgC/hr/µg Chl a	µgC/l/hr	µg/l	µgC/hr/µg Chl a	L/min	EST
	1600	0.5	37.55	11.48	3.27	31.33	7.93	3.95	.218	1725
		1.0	23.94	11.65	2.05	20.85	9.28	2.24	.124	
		2.0	6.87	10.63	.64	8.26	7.60	1.08	.051	
		4.0	3.65	8.52	.43	2.71	6.37	.42	.011	

Table B1 (Continued).

DATE	TIME EST	DEPTH m	TOTAL PHYTOPLANKTON PRIM PROD µgC/l/hr	CHL a µg/l	ASSIM RATIO µgC/hr/µg Chl a	NANNOPLANKTON PRIM PROD µgC/l/hr	CHL a µg/l	ASSIM RATIO µgC/hr/µg Chl a	INC LIGHT L/min	INC TIME EST
23 VII 74	0400	0.5	10.82	15.70	.69	11.31	12.41	.91	.147	0600
		1.0	4.23	16.84	.25	1.95	10.38	.187	.077	
		2.0	-	16.84	-	-	12.07	-	.018	
		4.0	3.54	16.08	.22	1.38	11.82	.116	.001	
	0600	0.5	31.69	11.65	2.72	17.46	14.23	1.65	.315	0735
		1.0	23.10	14.05	1.64	23.96	11.23	2.13	.187	
		2.0	9.86	12.15	.81	4.59	9.28	.49	.047	
		4.0	-	11.98	-	1.05	9.03	.116	.005	
	0800	0.5	61.33	15.57	3.94	32.83	12.49	2.63	.489	0930
		1.0	29.57	16.58	1.78	21.74	12.32	1.76	.270	
		2.0	23.55	16.08	1.46	19.11	11.82	1.61	.062	
		4.0	2.60	13.80	.19	2.37	10.47	.220	.008	
	1000	0.5	36.86	16.96	2.17	33.15	10.51	3.15	.434	1100
		1.0	37.78	14.53	2.60	23.08	12.53	1.84	.254	
		2.0	13.26	15.83	.83	13.87	11.52	1.20	.064	
		4.0	4.43	13.29	.33	6.25	9.71	.64	.005	
	1100	0.5	15.77	18.99	2.93	48.85	13.67	3.57	.353	1200
		1.0	35.66	28.70	1.24	20.91	16.84	1.24	.181	
		2.0	19.35	23.00	.84	13.21	16.46	.80	.045	
		4.0	1.76	16.58	.10	.82	11.82	.07	.004	
	1200	0.5	35.88	18.23	1.97	28.12	10.51	3.62	.330	1345
		1.0	49.34	15.19	3.25	37.79	12.79	2.95	.165	
		2.0	13.59	14.53	.93	12.09	13.80	.87	.044	
		4.0	1.77	16.96	.10	2.88	9.20	.31	.004	

Table B1 (Continued).

DATE	TIME	DEPTH	TOTAL PHYTOPLANKTON PRIM PROD	TOTAL PHYTOPLANKTON CHL a	TOTAL PHYTOPLANKTON ASSIM RATIO	NANNOPLANKTON PRIM PROD	NANNOPLANKTON CHL a	NANNOPLANKTON ASSIM RATIO	INC LIGHT	INC TIME
	EST	m	µgC/1/hr	µg/1	µgC/hr/µg Chl a	µgC/1/hr	µg/1	µgC/hr/µg Chl a	L/min	EST
	1400	0.5	43.19	16.88	2.56	23.91	10.13	2.36	.151	1546
		1.0	20.31	17.09	1.19	16.42	10.72	1.53	.075	
		2.0	4.59	14.94	.31	8.56	9.79	.87	.021	
		4.0	-	14.81	-	-	9.28	-	.003	
	1600	0.5	11.15	23.00	.48	12.24	13.67	.89	.055	1740
		1.0	12.25	19.41	.63	4.85	13.67	.35	.022	
		2.0	2.52	16.96	.15	2.15	10.72	.20	.007	
		4.0	1.05	12.32	.08	1.18	8.61	.32	.001	

Table B1 (Continued).

DATE	TIME EST	DEPTH m	TOTAL PHYTOPLANKTON PRIM PROD µgC/l/hr	CHL a µg/l	ASSIM RATIO µgC/hr/µg Chl a	NANNOPLANKTON PRIM PROD µgC/l/hr	CHL a µg/l	ASSIM RATIO µgC/hr/µg Chl a	INC LIGHT L/min	INC TIME EST
21 VIII 74	0500	0.5	3.45	10.47	.32	5.14	9.28	.55	.042	0610
		1.0	1.87	10.38	.18	-	8.44	-	.023	
		2.0	.48	10.89	.04	1.63	9.28	.17	.006	
		4.0	.51	10.21	.05	-	8.02	-	.0013	
	0600	0.5	12.71	9.20	1.38	12.75	6.41	1.98	.149	0745
		1.0	12.18	8.61	1.41	14.34	6.75	2.12	.093	
		2.0	7.50	7.85	.95	4.42	6.25	.70	.023	
		4.0	.39	7.51	.05	2.01	5.65	.35	.0046	
	0800	0.5	22.57	9.37	2.40	19.26	7.26	2.65	.180	0950
		1.0	21.19	9.62	2.20	16.37	6.92	2.36	.127	
		2.0	7.81	8.95	.87	7.62	7.76	.98	.037	
		4.0	2.43	9.12	.26	2.30	6.33	.36	.0053	
	1000	0.5	23.88	11.52	2.94	21.79	8.61	2.53	.184	1150
		1.0	27.33	13.42	2.03	27.11	11.01	2.46	.132	
		2.0	17.21	13.67	1.25	14.36	9.62	1.49	.035	
		4.0	2.58	11.82	.21	2.93	9.03	.32	.0051	
	1200	0.5	27.28	10.80	2.52	19.74	7.34	2.68	.164	1340
		1.0	21.54	11.52	1.86	17.75	8.36	2.12	.125	
		2.0	10.62	10.97	.96	8.71	8.36	1.04	.029	
		4.0	2.44	11.14	.21	2.26	8.02	.28	.0048	
	1400	0.5	15.32	14.43	1.06	12.59	10.38	1.21	.059	1550
		1.0	16.60	17.98	.92	16.54	15.07	1.09	.044	
		2.0	7.92	17.98	.44	5.02	12.66	.39	.009	
		4.0	2.42	12.66	.19	1.13	9.79	.11	.0018	

Table B1 (Continued).

DATE	TIME	DEPTH	TOTAL PHYTOPLANKTON PRIM PROD	TOTAL PHYTOPLANKTON CHL a	TOTAL PHYTOPLANKTON ASSIM RATIO	NANNOPLANKTON PRIM PROD	NANNOPLANKTON CHL a	NANNOPLANKTON ASSIM RATIO	INC LIGHT	INC TIME
	EST	m	µgC/l/hr	µg/l	µgC/hr/µg Chl a	µgC/l/hr	µg/l	µgC/hr/µg Chl a	L/min	EST
	1600	0.5	.42	10.13	-	.41	8.10	.05	.002	1800
		1.0	.81	10.13	-	.29	8.02	.03	.001	
		2.0	2.32	9.03	.25	1.32	7.01	-	.001	
		4.0	-	11.39	-	-	8.86	-	.0001	

Table B1 (Continued).

DATE	TIME EST	DEPTH m	TOTAL PHYTOPLANKTON PRIM PROD µgC/l/hr	CHL a µg/l	ASSIM RATIO µgC/hr/µg Chl a	NANNOPLANKTON PRIM PROD µgC/l/hr	CHL a µg/l	ASSIM RATIO µgC/hr/µg Chl a	INC LIGHT L/min	INC TIME EST
1 X 74	0600	0.5	29.49	16.9	1.74	29.32	13.7	2.14	.209	0845
		1.0	16.08	12.2	1.32	22.00	12.7	1.73	.136	
		2.0	7.91	14.1	.56	11.49	14.8	.77	.046	
		4.0	1.24	12.3	.100	1.08	14.9	.07	.008	
	0800	0.5	50.32	20.1	2.50	52.76	19.3	2.73	.446	1040
		1.0	51.57	22.5	2.29	50.53	21.7	2.33	.301	
		2.0	53.22	26.1	2.04	45.72	20.5	2.23	.106	
		4.0	9.32	26.7	.349	10.91	22.3	.49	.017	
	1000	0.5	57.39	23.8	2.41	47.91	17.9	2.67	.595	1240
		1.0	61.99	17.2	3.60	54.56	21.6	2.53	.373	
		2.0	47.25	25.0	1.89	39.28	20.8	1.88	.116	
		4.0	8.08	27.6	.293	10.18	25.1	.40	.016	
	1200	0.5	61.68	14.3	4.31	55.13	17.2	3.20	.495	1440
		1.0	66.02	25.0	2.64	60.57	27.0	2.24	.266	
		2.0	54.53	18.7	2.92	49.07	18.3	2.68	.081	
		4.0	8.77	25.3	.347	4.39	21.3	.20	.010	
	1400	0.5	44.36	20.6	2.15	44.30	19.8	2.24	.127	1640
		1.0	43.83	18.5	2.37	35.28	18.9	1.87	.062	
		2.0	15.75	11.4	1.38	17.88	15.2	1.76	.024	
		4.0	3.25	13.5	.241	2.85	9.5	.30	.002	
	1600	0.5	16.77	21.3	.79	12.85	34.5	.37	.031	1830
		1.0	4.16	27.6	.151	6.46	18.5	.35	.016	
		2.0	4.28	20.2	.212	3.20	18.7	.17	.005	
		4.0	3.06	16.8	.182	3.22	14.0	.23	.001	

Table B1 (Continued).

DATE	TIME EST	DEPTH m	TOTAL PHYTOPLANKTON PRIM PROD µgC/l/hr	CHL a µg/l	ASSIM RATIO µgC/hr/µg Chl a	NANNOPLANKTON PRIM PROD µgC/l/hr	CHL a µg/l	ASSIM RATIO µgC/hr/µg Chl a	INC LIGHT L/min	INC TIME EST
13 XI 74	0600	0.5	4.67	3.79	1.23	4.94	2.59	1.91	.285	0810
		1.0	4.13	2.67	1.54	5.26	3.75	1.40	.225	
		2.0	3.41	4.43	.77	5.45	2.82	1.93	.075	
		4.0	1.79	4.17	.43	1.34	3.33	.40	.025	
	0800	0.5	5.33	3.67	1.45	5.03	3.84	1.31	.469	0945
		1.0	7.27	4.47	1.62	8.08	2.91	2.77	.348	
		2.0	-	3.84	-	6.72	3.67	1.83	.159	
		4.0	2.61	4.13	.63	2.55	3.33	.76	.053	
	1000	0.5	8.86	4.60	1.93	5.96	3.42	1.74	.566	1140
		1.0	6.31	4.97	1.26	6.70	3.84	1.74	.430	
		2.0	8.52	4.55	1.87	6.74	2.49	2.71	.230	
		4.0	6.57	5.02	1.31	4.67	3.54	1.32	.073	
	1200	0.5	8.96	4.22	2.12	7.93	4.43	1.79	.399	1340
		1.0	10.56	4.85	2.18	7.72	3.37	2.29	.227	
		2.0	6.69	5.06	1.32	4.99	4.55	1.09	.124	
		4.0	4.23	5.27	.80	3.49	4.34	.80	.041	
	1400	0.5	5.82	3.37	1.73	3.03	2.57	1.18	.186	1540
		1.0	4.40	3.75	1.17	2.18	2.53	.86	.084	
		2.0	1.97	3.46	.57	.16	2.95	.05	.040	
		4.0	.51	3.79	.13	.42	2.87	.15	.006	

Table B2. Environmental data for the lower York River for 1974. Date, time and depth of sample collection are shown. Variables include salinity, temperature, dissolved oxygen, light transmittance and chlorophyll "a" for both the total and nannoplankton (<15μm).

Time (EST)	Depth (m)	Salinity (o/oo)	Temp (°C)	Dissolved Oxygen (mg/l)	Dissolved Oxygen (% sat)	Light Trans. (%)	Chlorophyll a (µg/l) Total	Chlorophyll a (µg/l) <15 µm
			11 February 1974					
0600	0.5	-	-				7.99	3.64
	1	17.01	5.0	10.6	93		5.07	2.87
	2	17.01	5.0				4.97	2.77
	4	17.01	5.5				2.31	3.84
	6	17.00	5.5					
	8	17.00	5.7					
	10	17.17	5.5	10.5	93			
	12	17.37	4.0					
	14	17.84	5.1					
	16	18.75	4.5					
	18	19.00	5.1	9.6	95			
0800	0.5	-	-				2.70	3.65
	1	16.99	5.8	10.3	91		4.10	3.96
	2	16.94	6.0				6.80	3.41
	4	16.94	6.0				5.08	3.02
	6	16.90	6.0					
	8	17.00	6.0					
	10	17.12	6.0	10.6	96			
	12	17.18	6.0					
	14	17.33	6.0					
	16	17.37	6.0					
	17	17.56	6.0	10.7	96			
1000	0.5	-	-			72	4.86	3.81
	1	17.10	7.0	10.7	99	52	7.34	4.09
	2	17.08	7.0			27	8.64	3.79
	4	16.25	6.5			7.0	5.72	3.61
	6	16.32	6.0					
	8	17.08	6.0					
	10	17.12	6.0	10.6	95			
	12	17.12	6.0					
	14	17.34	6.0					
	16	17.78	6.0	10.5	95			
1200	0.5	-	-			81	5.29	3.42
	1	17.17	7.0	10.7	99	65	5.62	3.33
	2	17.15	6.0			42	5.51	3.54
	4	17.16	6.0			18	7.02	4.22
	6	17.16	6.0					
	8	17.15	5.8					
	10	17.15	5.5	10.6	94			
	12	17.17	6.0					
	14	17.19	5.5					
	16	17.46	6.0					
	17	17.63	6.0	10.5	95			

1400	0.5	-	-			71	5.51	3.63
	1	17.22	6.0	10.8	98	50	7.67	3.50
	2	17.23	6.5			25	10.66	3.21
	4	17.23	6.5			6.0	8.21	2.66
	6	17.23	6.0					
	8	17.23	6.0					
	10	17.23	6.5	10.8	99			
	12	17.52	6.5					
	14	17.56	6.5					
	16	17.91	6.0	10.1	91			
1600	0.5	-	-			66	8.96	2.91
	1	17.32	6.0	11.2	100	44	6.05	3.04
	2	17.30	6.0			19	7.99	3.04
	4	17.29	6.0			4.0	5.94	2.87
	6	17.29	6.0					
	8	17.28	6.0					
	10	17.30	6.0	10.7	96			
	12	17.54	6.0					
	14	18.35	6.0					
	16	18.61	6.0	10.4	94			
1800	1	17.11	2.0	11.2	91		8.93	4.22
	2	17.13	2.0					
	4	17.13	5.0				3.78	3.46
	6	17.13	5.0					
	8	17.13	5.0					
	10	17.14	5.5	9.8	87			
	12	17.22	5.5					
	14	19.59	5.2					
	16	19.65	5.0					
	18	20.74	5.5	9.7	88			
2000	1	17.06	4.0	7.8	66		3.56	3.71
	2	16.98	3.0					
	4	16.99	5.0				8.42	3.63
	6	16.97	5.0					
	8	17.04	4.0					
	10	17.02	5.0	10.7	94			
	12	18.62	5.0					
	14	18.88	5.0					
	16	18.93	5.0					
	18	19.64	5.0	9.7	86			

2200	1	17.08	5.0	10.2	89	7.24	2.95
	2	16.89	2.0				
	4	17.03	5.0			5.83	4.14
	6	17.03	4.0				
	8	17.89	5.0				
	10	18.05	5.0	8.4	74		
	12	18.79	2.0				
	14	19.16	6.0				
	16	19.59	5.0				
	18	20.54	4.0	9.3	80		
				12 February 1974			
2400	1	17.18	4.0	8.5	73	7.00	3.92
	2	17.08	5.0				
	4	17.08	5.0			9.07	3.97
	6	17.11	5.0				
	8	17.22	5.0				
	10	17.26	5.0	10.7	94		
	12	18.29	5.0				
	14	18.37	4.8				
	16	20.50	5.0				
	18	23.01	5.0	8.9	81		
0200	1	17.23	5.0	10.8	95	2.70	4.47
	2	17.20	5.0				
	4	17.20	5.8			3.89	3.96
	6	17.21	5.0				
	8	17.33	5.2				
	10	17.46	5.5	10.6	94		
	12	18.21	4.0				
	14	18.71	4.0				
	16	19.62	5.0				
	18	22.33	5.5	10.3	94		
0400	1	17.17	6.0	10.5	94	3.67	3.21
	2	17.05	5.0				
	4	16.96	5.0			6.91	3.97
	6	17.07	5.0				
	8	17.22	6.0				
	10	17.41	6.0	10.5	94		
	12	19.16	5.0				
	14	18.18	6.0				
	16	21.06	5.5				
	18	22.40	5.5	9.6	88		

0600	1	16.85	2.5	11.2	92	11.52	2.45
	2	16.75	5.0				
	4	16.73	5.0			11.81	3.88
	6	16.72	5.0				
	8	16.71	5.0				
	10	17.29	6.0	10.9	98		
	12	17.90	5.0				
	14	20.32	5.0				
	16	21.88	5.0	9.0	81		

Time (EST)	Depth (m)	Salinity (o/oo)	Temp (°C)	Dissolved Oxygen (mg/l)	Dissolved Oxygen (% sat)	Light Trans. (%)	Chlorophyll a (µg/l) Total	Chlorophyll a (µg/l) <15 µm
				16 April 1974				
0500	0.5	15.65	-	-			7.43	5.57
	1	15.58	-	-			7.60	4.98
	2	15.74	-	-			7.17	5.36
	4	15.71	-	-			7.26	5.19
	6							
	8							
	10	18.37	-	-				
	12							
	14							
	16							
	18							
	20B	27.24	-	-				
0700	0.5	15.76	13.5	9.85	104	55	6.03	5.11
	1	15.63	13.5	9.97	105	36	8.27	5.11
	2	15.83	13.5	9.89	104	20	7.60	5.32
	4	16.66	13.5	9.95	105	5.7	8.19	5.65
	6					0.4		
	8							
	10	18.57	12.5	9.25	97			
	12							
	14							
	16							
	18							
	20B	24.94	10.5	7.56	79			
0800	0.5					37	5.74	3.80
	1	14.86	14.0			28	5.70	4.09
	2					14.6	6.67	4.94
	4	15.86	13.5			3.9	7.85	-
	6					1.2		
	8					.3		
	10	20.98	11.0					
	12							
	14							
	16							
	18							
	20B	26.81	10.5					
0900	0.5	14.99	14.0	9.95	105	59	7.43	4.43
	1	14.77	14.2	9.79	104	40	6.41	4.01
	2	14.81	14.2	9.85	104	16.8	8.02	4.64
	4	15.08	13.7	9.27	97	4.2	9.54	7.34
	6							
	8							
	10	19.45	11.1	8.06	82			
	12							
	14							
	16							
	18							
	20B	26.71	10.5	7.64	81			

1100	0.5	15.48	14.5	10.25	111	57	7.93	5.74
	1	15.30	14.5	10.39	112	37	7.60	6.16
	2	15.33	14.2	10.07	107	18.8	9.20	7.60
	4	15.37	14.0	9.83	105	3.5	17.22	9.45
	6					.8		
	8					.2		
	10	18.21	12.0	8.28	86			
	12							
	14							
	16							
	18							
	20B	27.21	11.0	7.34	81			
1300	0.5	14.53	15.5	10.94	120	53	10.47	7.17
	1	14.30	15.0	10.94	118	36	13.00	10.46
	2	14.93	14.8	11.14	120	14	17.22	10.80
	4	15.15	14.0	10.49	111	2.5	17.22	9.96
	6					.7		
	8					.2		
	10	18.82	12.0	8.86	92			
	12							
	14							
	16							
	18							
	20B	27.18	10.5	7.72	82			
1400	0.5					53		
	1	14.62	15.3			35	9.96	-
	2					15.8		
	4	16.97	13.5			1.8	12.91	-
	6					.6		
	8					.2		
	10	19.23	12.3					
	12							
	14							
	16							
	18							
	20B	26.92	10.9					
1500	0.5	14.23	16.0	11.16	123	49	7.85	3.71
	1	14.15	15.7	11.44	125	35	8.36	5.23
	2	14.41	15.3	11.82	128	14	9.62	5.15
	4	14.77	14.0	9.47	100	1.8	15.95	7.09
	6					.5		
	8					.1		
	10	19.59	12.0	7.82	82			
	12							
	14							
	16							
	18							
	20B	27.06	10.5	7.32	77			

1700	0.5	14.24	15.0	11.04	119	54	8.86	4.81
	1	14.33	15.0	11.02	119	36	9.96	5.82
	2	14.22	14.5	11.02	107	14.8	9.12	5.23
	4	16.07	14.0	10.65	114	3.3	15.70	6.50
	6					1.0		
	8					.2		
	10	17.58	13.0	9.25	97			
	12							
	14							
	16							
	18							
	20B	26.64	-	7.28	77			
1900	0.5					56		
	1	16.13	14.8	10.84	117	40	7.60	4.52
	2					14.7		
	4	14.56	13.8	10.21	107	4	17.85	8.19
	6					.8		
	8					.3		
	10	16.36	12.0	8.56	88			
	12							
	14							
	16							
	18							
	20B	19.98	10.5	7.58	77			
2000	0.5							
	1	14.30	14.6				4.64	4.13
	2							
	4	14.91	13.8				10.46	6.67
	6							
	8							
	10	20.06	11.8					
	12							
	14							
	16							
	18							
	20B	26.74	10.8					
2100	0.5							
	1	14.77	14.77	10.55	113		5.99	4.05
	2							
	4	15.69	15.69	10.77	115		9.12	5.65
	6							
	8							
	10	19.03	19.03	8.78	91			
	12							
	14							
	16							
	18							
	20B	20.47	20.47	7.16	73			

2300	0.5						
	1	13.93	15.0	10.53	113	4.90	3.54
	2						
	4	17.17	13.0	10.15	107	20.68	9.28
	6						
	8						
	10	18.91	11.0	7.46	76		
	12						
	14						
	16						
	18						
	20B	27.07	10.5	7.46	79		
				17 April 1974			
0200	0.5						
	1	13.40	14.5	10.57	112	4.22	3.12
	2						
	4	16.68	13.5	10.27	108	28.70	12.41
	6						
	8						
	10	25.50	10.5	7.68	81		
	12						
	14						
	16						
	18						
	20B	26.90	10.5	6.90	73		
0300	0.5						
	1	13.49	14.5	10.56	112	4.47	3.29
	2						
	4	16.39	13.5	10.38	110	11.4	6.58
	6						
	8						
	10	22.90	11.0	7.50	78		
	12						
	14						
	16						
	18						
	20B	27.20	10.5	7.90	84		
0500	0.5						
	1	16.37	14.0	10.24	109	7.68	5.61
	2						
	4	21.48	13.8	10.22	112	10.50	9.96
	6						
	8						
	10	22.16	11.5	7.78	81		
	12						
	14						
	16						
	18						
	20B	27.34	10.5	6.94	74		

0800	0.5						
	1	15.11	14.2	10.60	113	5.23	4.90
	2						
	4	16.22	14.1	10.40	112	7.73	6.35
	6						
	8						
	10	20.85	12.0	8.00	84		
	12						
	14						
	16						
	18						
	20B	27.37	10.8	7.08	75		

Time (EST)	Depth (m)	Salinity (o/oo)	Temp (°C)	Dissolved Oxygen (mg/l)	Dissolved Oxygen (% sat)	Light Trans. (%)	Chlorophyll a (µg/l) Total	Chlorophyll a (µg/l) <15 µm
				21 May 1974				
0500	0.5	16.74	20.5	8.55	105		9.28	4.52
	1	16.73	20.5	8.33	102		10.38	3.80
	2	16.73	20.5	8.61	106		10.80	3.12
	4	16.73	20.5	8.51	104		10.47	3.33
	10	18.29	19.5	5.88	71			
	18	22.48	16.1	2.83	33			
0700	0.5	16.51	20.1	8.63	105	43	13.80	4.98
	1	16.50	20.5	8.61	106	30	11.27	4.18
	2	16.51	20.5	8.26	104	13	11.14	2.77
	4	16.53	20.5	8.73	107	2.3	11.27	4.56
	10	17.98	19.5	6.24	75			
	18	22.70	16.1	2.51	29			
0900	0.5	16.44	20.1	8.63	105	46	11.48	4.43
	1	16.41	20.2	8.97	109	33	12.15	4.35
	2	16.35	20.1	9.50	116	11	13.25	4.64
	4	16.39	20.1	9.05	110	2.0	12.15	5.06
	10	16.82	19.5	7.92	95			
	18	22.91	16.1	2.49	29			
1100	0.5	16.40	20.3	9.23	112	53	12.53	6.54
	1	16.17	20.7	9.21	113	40	11.27	5.91
	2	16.20	20.8	9.25	114	18	12.66	5.28
	4	16.17	20.0	9.21	112	3.8	14.18	7.51
	10	18.18	19.2	6.06	73			
	18	21.28	17.0	2.85	33			
1300	0.5	16.39	21.0	9.32	115	40	11.39	4.52
	1	16.39	21.0	10.51	130	34	12.15	4.81
	2	16.52	20.5	9.21	113	20	7.43	5.32
	4	16.67	20.3	8.67	106	3.4	11.39	4.60
	10	18.28	19.0	5.29	66			
	18	22.15	16.3	2.37	27			
1500	0.5	16.66	21.0	9.31	115	46	13.67	6.16
	1	16.63	21.0	9.19	114	34	11.77	5.36
	2	16.71	21.0	9.36	116	19	11.14	5.53
	4	16.65	21.0	9.32	115	4.1	12.41	7.60
	10	18.26	19.5	5.31	64			
	18	23.04	16.4	2.29	27			
1700	0.5	16.25	21.0	9.31	115	52	8.74	3.86
	1	16.73	21.0	9.19	114	30	9.92	3.70
	2	16.73	21.0	9.32	115	13	7.85	2.75
	4	16.73	21.0	9.72	120	2.6	5.87	5.11
	10	18.04	19.6	9.35	113			
	18	21.85	17.0	2.81	33			

1900	1	16.27	20.7	9.66	118	35	10.08	3.63
	2	16.31	20.7	9.99	123	15		
	4	16.37	20.7	9.88	121	3.3	9.12	3.58
	6	16.41	20.8	9.70	119	0.6		
	8	16.45	20.9	9.54	117			
	10	16.60	20.6	9.05	111			
	12	20.85	17.5	3.66	43			
	14	21.68	17.0	2.71	32			
	16	22.60	16.8	2.28	26			
2100	1	16.18	20.2	9.25	112		11.70	3.12
	2	16.17	20.2	9.60	116			
	4	16.18	20.2	9.25	112		10.28	3.26
	6	16.17	20.2	9.82	119			
	8	16.18	20.2	9.19	111			
	10	19.43	18.3	4.75	56			
	18	19.47	18.1	4.65	55			
2300	1	15.82	20.1	9.70	117		11.39	5.44
	2	15.90	20.1	9.50	114			
	4	16.04	20.0	9.32	112		10.94	4.51
	6	16.13	19.9	9.25	111			
	8	17.45	20.0	7.78	94			
	10	17.91	19.4	6.43	77			
				22 May 1974				
0100	1	16.23	20.1	9.27	112		10.63	5.40
	2	16.25	20.1	9.36	114			
	4	16.32	20.1	8.97	109		11.01	5.02
	6	16.54	20.1	8.51	103			
	8	17.02	20.1	7.62	93			
	10	17.74	19.9	6.02	73			
	12	19.14	19.0	4.67	56			
0300	1	16.61	20.2	8.49	103		11.14	4.52
	2	16.62	20.2	8.61	105			
	4	17.41	20.2	6.47	78		11.90	7.09
	6	17.61	19.9	6.10	74			
	8	17.92	19.5	5.17	62			
	10	18.17	19.0	5.05	60			

Time (EST)	Depth (m)	Salinity (o/oo)	Temp (°C)	Dissolved Oxygen (mg/1)	Dissolved Oxygen (% sat)	Light Trans. (%)	Chlorophyll a (µg/1) Total	Chlorophyll a (µg/1) <15 µm
			18 June 1974					
0400	0.5	17.17	23.8	7.94	104		8.27	4.52
	1	17.29	23.3	7.16	94		9.96	5.78
	2	17.24	23.3	7.26	95		9.62	5.65
	4	17.22	23.3	7.14	93		9.28	5.36
	6	17.61	23.4	6.55	86			
	8	23.30	21.7	2.07	27			
	10	24.72	21.3	1.61	21			
	12	25.74	21.1	1.41	18			
	14	26.19	21.0	1.51	19			
	16	26.35	21.0	1.31	17			
	17.5B	26.60	21.0	1.27	17			
0600	0.5	17.16	23.8	7.84	101	61	6.16	4.47
	1	17.16	23.8	7.82	101	43	7.09	4.71
	2	17.19	23.8	7.76	100	15	5.99	4.68
	4	17.18	23.4	7.78	100	3.3	7.60	4.19
	6	17.59	23.2	6.53	84	0.5		
	8	19.60	22.7	4.22	54			
	10	21.05	22.0	3.12	40			
	12	24.95	21.1	3.72	48			
	14	25.59	21.0	1.61	21			
	16	26.38	21.0	1.45	19			
	18	26.71	21.0	1.29	17			
	19B	26.69	21.0	1.41	18			
0800	0.5	17.28	23.8	7.98	104	54	6.58	5.74
	1	17.19	23.5	7.94	104	36	8.62	6.41
	2	17.19	23.5	7.92	103	13	8.61	5.91
	4	17.20	23.5	7.94	104	2.5	8.69	7.51
	6	17.56	23.5	6.63	86	0.6		
	8	18.55	23.1	5.33	69			
	10	19.43	22.8	4.22	55			
	12	25.06	21.1	1.51	20			
	14	25.51	21.0	1.53	20			
	16	26.50	21.0	1.41	18			
	18	26.56	21.0	1.27	16			
	19.5B	26.72	21.0	1.21	16			

1000	0.5	17.24	24.5	8.44	111	44	7.85	5.91
	1	17.12	24.5	8.06	106	31	8.27	6.67
	2	17.24	24.2	8.24	108	14	9.71	6.33
	4	17.28	24.0	7.40	97	2.3	9.54	7.34
	6	17.72	23.9	6.35	84	0.5		
	8	18.93	23.4	4.54	59			
	10	22.24	22.2	2.53	33			
	12	25.36	21.3	1.37	18			
	14	25.83	21.2	1.41	18			
	16	26.31	21.1	1.21	16			
	18	26.45	21.0	1.27	16			
	19SB	26.56	21.0	1.41	18			
1200	0.5	17.28	24.9	8.72	116	52	8.44	6.03
	1	17.26	24.8	8.61	115	36	11.39	6.08
	2	17.29	24.5	8.84	118	17	10.55	5.65
	4	17.32	24.2	8.32	111	2.7	10.13	6.20
	6	17.29	24.0	7.34	98	0.5		
	8	17.94	23.5	7.08	92			
	10	23.87	21.9	1.90	25			
	12	25.40	21.5	1.41	18			
	14	26.15	21.0	1.21	16			
	16	26.18	21.0	1.23	15			
	18B	26.30		1.56	20			
1400	0.5	17.33	24.8			41	12.49	12.41
	1	17.33	24.7	8.34	111	28	11.65	13.08
	2	17.34	24.1	8.16	109	9.0	12.91	11.65
	4	17.62	23.9	6.75	89	1.3	15.57	9.45
	6	18.72	23.3			0.2		
	8	22.29	22.3					
	10	25.28	21.1	1.41	18			
	12	26.17	21.0					
	14	26.26	21.0					
	16	26.27	21.0					
	18	26.57	21.0					
	19B	26.58	20.9	1.18	15			
1600	0.5	17.38	24.8			39	11.48	7.93
	1	17.38	24.8	8.86	119	20	11.65	9.28
	2	17.36	24.8	9.00	121	6.5	10.63	7.60
	4	17.35	24.2	8.66	116	1.2	8.52	6.37
	6	17.85	24.0			0.1		
	8	19.74	23.2					
	10	24.07	21.8	1.67	22			
	12	24.83	21.3					
	14	25.79	21.0					
	16	26.15	21.0					
	18SB	26.22	21.0	1.00	13			

1800	0.5	17.53	24.0			59	8.02	5.49
	1	17.33	24.8	9.35	126	38	8.36	5.44
	2	17.32	24.8	8.76	118	17	7.25	4.39
	4	17.31	24.8	8.74	118	5.0	8.36	5.15
	6	17.38	24.3			0.9		
	8	17.59	24.0					
	10	19.26	23.2	4.26	56			
	12	19.50	23.0					
	14	22.31	22.5					
	16	22.44	22.0					
	17B	25.45	21.5	1.31	17			
2000	0.5	17.56	24.1					
	1	17.42	24.1	8.62	113		4.73	3.33
	2	17.36	24.1	8.64	114			
	4	17.36	24.1	8.60	113		4.98	3.12
	6	17.99	23.5					
	8	18.10	23.5					
	10	18.20	23.2	5.73	75			
	12	23.92	22.1					
	14	24.75	21.5					
	16	25.93	21.1					
	18B	26.17	21.1	1.37	18			
2200	0.5	17.40	24.1					
	1	17.35	24.1	8.72	115		4.43	3.46
	2	17.37	24.1	8.34	110			
	4	17.69	24.0	7.27	96		6.46	4.77
	6	17.69	23.8					
	8	17.92	23.8					
	10	23.05	22.0	2.58	34			
	12	24.01	21.5					
	14	25.20	21.2					
	16	25.75	21.1					
	18.5B	25.97	21.0	1.5	20			
2400	0.5	17.56	24.0					
	1	17.38	24.0	8.34	110		5.36	4.01
	2	17.37	24.0	8.24	108			
	4	17.47	24.0	7.74	102		6.20	4.26
	6	17.70	23.9					
	8	18.52	23.3					
	10	20.84	22.5	3.22	42			
	12	22.50	22.0					
	14	23.88	21.7					
	16	25.71	21.2					
	18.5	25.75	21.1	1.33	17			

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0200	0.5	17.34	23.5					
	1	17.33	24.0	8.28	109		4.90	3.54
	2	17.33	24.0	8.54	113			
	4	17.34	24.0	8.34	110		5.11	4.01
	6	18.55	24.0					
	8	19.80	24.0					
	10	22.58	22.0	2.51	33			
	12	24.28	21.9					
	14	25.30	21.4					
	16	25.63	21.1					
	18B	25.64	21.1	1.21	16			
0400	0.5	17.39	24.0					
	1	17.38	24.0	7.84	104		6.25	5.15
	2	17.38	24.0	8.04	106			
	4	18.16	23.9	6.63	88		8.36	5.61
	6	18.24	23.5					
	8	20.86	22.7					
	10	23.98	21.4	1.55	20			
	12	25.00	21.2					
	14	25.33	21.1					
	16B	25.66	21.1	1.12	14			
0600	0.5	17.64	24.0					
	1	17.44	24.0	7.74	102		7.76	5.49
	2	17.49	23.9					
	4	17.54	23.8	7.34	97		9.20	7.26
	6	17.55	23.8					
	8	17.65	23.7					
	10	17.97	22.2	2.81	36			
	12	21.89	21.9					
	14	23.26	21.5					
	16	24.70	21.5					
	18	25.04	21.3					
	19B	25.29	21.2	1.31	17			
0800	0.5	17.46	24.0			47		
	1	17.44	24.0	8.26	109	35	6.25	4.52
	2	17.46	23.9			17		
	4	17.63	23.9	7.34	96	3.2	4.26	5.65
	6	17.65	23.9			0.7		
	8	17.89	23.8					
	10	18.93	23.1	4.92	65			
	12	23.89	21.8					
	14	24.36	21.8					
	16	25.55	21.2					
	18	25.69	21.2					
	19.5B	25.79	21.2	0.88	12			

1000	0.5	17.50	25.0			49	5.78	4.68
	1	17.50	24.8	7.65	103	34	7.60	5.44
	2	17.49	24.8			13	7.01	5.23
	4	17.54	24.2	7.59	102	3.1	8.36	5.74
	6	17.55	24.0			0.6		
	8	17.65	24.0					
	10	21.21	23.0	5.12	68			
	12	23.25	22.2					
	14	24.72	21.8					
	16	25.43	21.2					
	18	25.56	21.2					
	19B	25.77	21.2	0.99	13			
1200	0.5	17.50	25.0			52		
	1	17.49	25.0	7.74	101	33	7.34	5.07
	2	17.53	24.2			15		
	4	17.62	24.0	5.76	77	2.7	9.79	6.16
	6	17.75	24.0					
	8	18.45	23.8					
	10	20.57	22.8	3.48	47			
	12	23.32	22.2					
	14	24.41	21.8					
	16	25.36	21.4					
	18B	25.40	21.4	1.13	15			
1400	0.5	17.61	21.7			39		
	1	17.57	21.7	7.65	96	20	11.56	7.60
	2	17.54	21.7			7.3		
	4	17.55	21.8	6.00	76	1.2	10.72	8.10
	6	18.14	21.2			0.1		
	8	19.11	21.0					
	10	21.57	20.1	2.38	30			
	12	23.52	19.9					
	14	25.21	19.1					
	15B	24.54	19.1					

Time (EST)	Depth (m)	Salinity (o/oo)	Temp (°C)	Dissolved Oxygen (mg/l)	Dissolved Oxygen (% sat)	Light Trans. (%)	Chlorophyll a (µg/l) Total	Chlorophyll a (µg/l) <15 µm
			23 July 1974					
0400	0.5	20.43	24.5	5.5	75		15.70	12.41
	1	20.43	25.0	5.5	75		16.84	10.38
	2	20.41	25.0	5.7	78		16.84	12.07
	4	20.40	25.0	5.8	79		16.08	11.82
	6	20.83	25.1	5.4	74			
	8	20.54	25.1	5.2	71			
	10	20.65	25.1	4.1	56			
	12	20.62	25.1	4.1	56			
	14	20.64	25.2	3.9	54			
	16	20.66	25.1	3.5	48			
0600	0.5	20.55	25.1	5.0	69	60	11.65	10.55
	1	20.52	25.2	5.1	70	30	14.05	11.23
	2	20.57	25.2	4.7	64	7.0	12.15	9.28
	4	20.59	25.2	4.6	63	0.67	11.98	9.03
	6	20.61	25.2	4.1	56	0.10		
	8	20.82	25.2	4.3	59			
	10	20.62	25.2	4.3	59			
	12	20.63	25.2	4.2	57			
	14	20.65	25.2	4.2	58			
	16	20.68	25.2	3.9	53			
		20.67	25.2	4.2	58			
0800	0.5	20.55	25.3	5.3	73	45	15.57	12.49
	1	20.54	25.3			28	16.58	12.32
	2	20.55	25.3	5.1	70	7.0	16.08	11.82
	4	20.79	25.3			0.79	13.80	10.47
	6	20.66	25.3	4.5	62			
	8	20.72	25.3	4.4	60			
	10	20.68	25.3					
	12	20.65	25.3	4.3	59			
	14	20.65	25.3	4.4	60			
	16	20.66	25.3					
		20.72	25.3	4.3	59			
1000	0.5	20.53	25.9	5.6	78	47	16.96	10.51
	1	20.52	25.9	5.9	82	27	14.35	12.53
	2	20.52	25.9	5.0	69	6.2	15.83	11.52
	4	20.51	25.2	4.8	66	0.74	13.29	9.71
	6	20.51	25.2	5.0	68			
	8	20.51	25.2	5.0	68			
	10	20.49	25.2	4.9	67			
	12	20.50	25.1	4.5	61			
	14	20.66	25.1	4.2	57			
	16	20.62	25.0	3.5	48			

1200	0.5	20.31	26.0	6.6	92	46	18.23	10.51
	1	20.31	26.0	6.9	96	26	15.19	12.79
	2	20.31	25.3	6.3	86	7.0	14.35	13.80
	4	20.35	25.1	5.9	81	0.88	16.96	9.20
	6	20.39	25.1	5.2	71			
	8	20.40	25.0	5.1	69			
	10	20.45	25.0	4.9	67			
	12	20.48	25.0	4.6	63			
	14	20.49	25.0	4.7	64			
	16	20.44	25.0	4.7	64			
		20.32	25.0	5.0	68			
1400	0.5	20.15	25.9	6.7	93	43	16.88	10.13
	1	20.11	25.2	6.6	90	19	17.09	10.72
	2	20.13	25.1	6.2	85	5.5	14.94	9.79
	4	20.20	25.0	6.2	84	0.42	14.81	9.28
	6	20.26	25.0	5.9	84			
	8	20.29	25.0	6.3	86			
	10	20.29	25.0	6.3	86			
	12	20.30	25.0	5.4	73			
	14	20.49	25.0					
	15	20.50	25.0	4.7	64			
		20.30	25.1	5.3	73			
1600	0.5	20.15	25.3	7.5	103	34	23.00	13.67
	1	20.11	25.2			18	19.41	13.67
	2	20.17	25.1	6.5	89	5.5	16.96	10.72
	4	20.29	25.1	6.3	86	0.56	12.32	8.61
	6	20.34	25.0	5.6	77			
	8	20.38	25.0	5.2	71			
	10	20.47	25.0	4.6	63			
	12	20.50	25.0	4.8	66			
	14	20.52	25.0	4.4	60			
	16	20.58	25.0	4.1	56			
		20.42	25.2	6.9				
1800	0.5	20.41	25.4	6.7	92	41	17.22	12.15
	1	20.39	25.4	6.8	93	16	15.70	10.89
	2	20.40	25.4	6.6	90	4.7	16.71	11.65
	4	20.45	25.2	5.7	78	0.42	9.03	7.85
	6	20.45	25.2	5.3	73			
	8	20.47	25.1	5.5	75			
	10	20.48	25.1	5.3	73			
	12	20.57	25.1	4.6	63			
	14	20.54	25.1	4.2	58			
	16	20.60	25.1	4.1	56			

2000	0.5	20.53	25.8	6.2	86	14.18	10.21
	1	20.53	25.8	6.3	87	14.31	10.47
	2	20.58	25.5	5.1	70	12.53	8.69
	4	20.63	25.3	4.5	62	11.27	7.68
	6	20.65	25.3	4.3	59		
	8	20.63	25.3	4.2	58		
	10	20.63	25.3	4.5	62		
	12	20.63	25.5	4.6	63		
	14	20.64	25.5	4.5	62		
	16	20.64	25.5	4.2	58		
		20.65	25.4	4.3			
2200	0.5	20.48	25.3	6.0	82	14.43	9.79
	1	20.49	25.2			11.90	8.78
	2	20.52	25.2	5.7	78	11.39	9.20
	4	20.48	25.2			12.58	8.95
	6	20.50	25.2	5.6	76		
	8	20.57	25.1	4.3	59		
	10	20.54	25.1				
	12	20.53	25.1	4.5	61		
	14	20.53	25.1	4.8	65		
	16	20.56	25.1				

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2400	0.5	20.23	25.0	6.1	83	8.86	7.76
	1	20.20	25.0	6.3	86	9.20	7.60
	2	20.24	25.0	5.8	79	9.79	7.34
	4	20.30	25.0	5.6	76	9.24	6.67
	6	20.30	25.1	5.9	80		
	8	20.34	25.1	5.6	76		
	10	20.30	25.1	5.3	72		
	12	20.33	25.1	5.2	71		
	14	20.38	25.1	4.9	67		
	16	20.36	25.2	4.7	64		

0200	0.5	20.19	25.0	5.3	72	8.44	6.50
	1	20.20	25.0	5.5	75	8.36	6.58
	2	20.18	24.9	5.4	74	8.36	6.41
	4	20.18	25.0	5.5	75	9.12	6.50
	6	20.19	25.0	5.5	75		
	8	20.20	25.0	5.6	76		
	10	20.20	25.0	5.5	75		
	12	20.22	25.0	5.4	74		
	14	20.26	25.0	5.0	68		
	16	20.34	25.1	4.9	67		
0400	0.5	20.07	25.0	5.7	78	11.73	8.69
	1	20.11	25.0	5.8	79	11.98	8.27
	2	20.15	25.0	5.8	79	10.76	8.27
	4	20.25	25.0	5.5	75	10.13	7.43
	6	20.28	25.0	5.3	72		
	8	20.36	25.0	4.9	67		
	10	20.19	25.0	5.0	68		
	12	20.40	25.0	4.9	67		
	14	20.45	25.0	4.6	63		
	16	20.46	25.1	4.3	58		
0600	0.5	20.42	25.0	5.0	68	15.32	9.03
	1	20.45	25.0	5.1	69	16.46	9.87
	2	20.46	25.2	5.0	68	15.19	9.71
	4	20.45	25.2	4.9	67	12.66	9.28
	6	20.46	25.2	5.0	68		
	8	20.46	25.2	5.1	69		
	10	20.50	25.2	4.7	64		
	12	20.48	25.2	4.9	67		
	14	20.47	25.2	4.6	63		
	16	20.48	25.2	4.9	67		
0800	0.5	20.54	25.1	4.7	64	11.82	8.44
	1	20.55	25.1	4.7	64	11.56	7.85
	2	20.52	25.2	4.8	65	12.58	7.93
	4	20.55	25.2	4.7	64	11.65	7.51
	6	20.56	25.2	4.5	61		
	8	20.57	25.2	4.6	63		
	10	20.57	25.2	4.3	59		
	12	20.60	25.2	4.5	61		
	14	20.57	25.2	4.5	61		
	16	20.59	25.2	4.4	60		

1000	0.5	20.45	24.5	4.7	64	11.23	8.44
	1	20.48	24.5	4.6	63	11.48	7.68
	2	20.48	25.0	4.6	64	10.72	8.02
	4	20.50	25.0	4.7	63	9.54	7.76
	6	20.49	25.0	4.6	64		
	8	20.52	25.0	4.7	64		
	10	20.53	25.1	4.7	64		
	12	20.53	25.1	4.7	64		
	14	20.54	25.1	4.6	63		
	16	20.58	25.1	4.4	60		
		20.43	25.5	4.3			
1200	0.5	20.30	24.9			12.28	
	1	20.23	24.9	5.5	75	16.46	
	2	20.23	24.9	5.6	77	17.09	
	4	20.22	24.9	5.4	74	17.22	
	6	20.29	25.0	5.0	68		
	8	20.30	25.0	4.9	67		
	10	20.32	25.0	4.6	63		
	12	20.31	25.0	4.5	61		
	14	20.33	25.0	4.5	61		
	16	20.33	25.1	4.5	61		
		20.30	25.1				
1400	0.5	20.05	25.0	6.1	83	18.36	
	1	20.04	25.0	6.1	83	17.09	
	2	20.03	25.0	6.0	82	13.17	
	4	20.08	25.0	5.9	80	13.55	
	6	20.11	25.0	6.0	82		
	8	20.10	25.0	6.1	83		
	10	20.15	25.0	5.8	79		
	12	20.12	25.0	5.5	75		
	14	20.14	25.0	5.4	73		
	16	20.15	25.0	5.2	71		

1600	0.5	20.06	25.0	5.7	78	14.50
	1	20.06	25.0	6.1	83	13.42
	2	20.07	25.0	5.9	80	13.67
	4	20.03	25.0	5.7	77	14.56
	6	20.02	25.0	5.7	78	
	8	20.03	25.0	5.6	76	
	10	20.07	25.0	5.7	78	
	12	20.07	25.1	5.1	69	
	14	20.15	25.1	4.9	67	
	16	20.26	25.1	4.7	64	

Time (EST)	Depth (m)	Salinity (o/oo)	Temp (°C)	Dissolved Oxygen (mg/1)	Dissolved Oxygen (% sat)	Light Trans. (%)	Chlorophyll a (µg/1) Total	Chlorophyll a (µg/1) <15 µm
				21 August 1974				
0400	0.5			6.4	87		10.47	9.28
	1	20.54	25.2	7.0	95		10.38	8.44
	2	20.52	25.0	6.8	93		10.89	9.28
	4	20.52	25.1	6.8	93		10.21	8.02
	6	20.57	25.2	5.6	77			
	8	20.56	25.2	5.6	77			
	10	20.56	25.2	7.0	96			
	12	20.58	25.2	5.6	77			
	14	20.58	25.2	6.2	85			
0600	0.5						9.20	6.41
	1	20.47	25.1	5.5	75		8.61	6.75
	2	20.47	25.1	5.7	78		7.85	6.25
	4	20.48	25.1	5.3	72		7.51	5.65
	6	20.52	25.1	5.4	74			
	8	20.53	25.1	5.4	74			
	10	20.55	25.1	5.5	75			
	12	20.54	25.1	5.4	74			
	14	20.60	25.1	5.2	71			
0800	0.5					33	9.37	7.26
	1	20.49	25.5	5.3	73	20	9.62	6.92
	2	20.49	25.5	5.2	72	5.0	8.95	7.76
	4	20.53	25.6	5.3	73	1.0	9.12	6.33
	6	20.54	25.6	5.2	72	.25		
	8	20.57	25.6	5.1	70			
	10	20.58	25.6	5.1	70			
	12	20.56	25.4	5.3	73			
	14	20.57	25.2	5.2	72			
1000	0.5			7.7	106	37	11.52	8.61
	1	20.58	25.9	6.4	88	25	13.42	11.01
	2	20.57	25.9	6.5	90	7.3	13.67	9.62
	4	20.58	25.7	6.5	90	1.1	11.82	9.03
	6	20.59	25.7	5.9	81	.10		
	8	20.58	25.5	5.6	77			
	10	20.60	25.5	6.5	89			
	12	20.67	25.3	5.1	70			
	14	20.68	25.2	6.8	94			

1200	0.5						10.80	7.34
	1	20.66	25.9	5.8	80		11.52	8.36
	2	20.67	25.9	5.6	77		10.97	8.36
	4	20.68	25.9	5.7	78		11.14	8.02
	6	20.68	25.8	5.6	77			
	8	20.69	25.5	5.8	80			
	10	20.71	25.2	5.2	72			
	12	20.69	25.2	5.2	72			
	14	20.69	25.2	5.3	73			
1400	0.5					45	14.48	10.38
	1	20.47	25.3	6.7	92	28	17.98	15.07
	2	20.48	25.2	6.6	91	5.8	17.98	12.66
	4	20.59	25.2	6.2	85	1.0	12.66	9.79
	6	20.64	25.2	6.1	84	.10		
	8	20.65	25.2	6.0	82			
	10	20.63	25.2	5.8	80			
	12	20.63	25.2	5.6	77			
	14	20.65	25.2	5.6	77			
1600	0.5			5.9	81		10.13	8.10
	1	20.58	25.3	6.4	88		10.13	8.02
	2	20.58	25.3	6.4	88		9.03	7.01
	4	20.56	25.3	6.5	89		11.39	8.86
	6	20.53	25.2	6.2	85			
	8	20.53	25.2	6.4	88			
	10	20.54	25.2					
	12	20.54	25.2	5.9	81			
	14	20.60	25.2					

1800	0.5					9.96	7.51
	1	20.51	25.2	5.7	78	10.47	7.68
	2	20.49	25.2	5.7	78	9.79	8.02
	4	20.50	25.2	5.6	77	9.71	7.82
	6	20.50	25.2	5.8	79		
	8	20.52	25.2	5.5	75		
	10	20.52	25.2	5.7	78		
	12	20.54	25.2	5.7	78		
	14	20.54	25.2	5.6	77		
2000	0.5					9.28	7.60
	1	20.46	25.2	5.3	72	8.78	7.17
	2	20.47	25.2	5.7	78	9.20	6.50
	4	20.46	25.2	5.5	75	9.28	6.50
	6	20.46	25.2	5.6	76		
	8	20.48	25.2	5.4	74		
	10	20.47	25.2	5.4	74		
	12	20.49	25.2	5.9	81		
	14	20.51	25.2	5.4	74		
2200	0.5					9.79	8.19
	1	20.52	25.2			10.30	7.93
	2	20.53	25.2			12.66	8.61
	4	20.56	25.2			12.91	10.04
	6	20.62	25.2	5.8	79		
	8	20.58	25.2	5.8	79		
	10	20.57	25.2				
	12	20.55	25.2	5.8	79		
	14	20.58	25.2				
			22 August 1974				
2400	0.5	20.57	25.0	5.6	76	9.54	7.76
	1	20.57	25.0	5.9	81	10.04	6.25
	2	20.57	25.1	6.2	85	9.54	6.33
	4	20.57	25.1	5.6	76	8.44	7.34
	6	20.57	25.0	5.6	77		
	8	20.58	25.1	5.6	76		
	10	20.58	25.1	5.5	75		
	12	20.58	25.0	5.9	81		
	14	20.56	25.0	5.6	76		

0200	0.5					7.60	5.99
	1	20.57	25.1	5.4	74	7.01	5.57
	2	20.57	25.1	5.6	76	7.68	5.82
	4	20.57	25.1	5.9	81	8.36	6.25
	6	20.56	25.1	5.4	74		
	8	20.57	25.1	5.7	78		
	10	20.57	25.1	5.4	74		
	12	20.58	25.1	5.7	78		
	14	20.59	25.1	6.1	83		
0400	0.5					7.76	7.68
	1	20.56	25.1	5.6	76	8.61	5.49
	2	20.55	25.1	6.0	82	9.37	7.34
	4	20.54	25.1	5.7	78	8.01	7.34
	6	20.52	25.0	6.0	82		
	8	20.54	25.0	5.8	79		
	10	20.54	25.0	5.1	69		
	12	20.54	25.0	5.9	81		
	14	20.54	25.0	5.8	79		
0600	0.5					6.84	7.01
	1	20.43	25.1	5.7	78	8.27	5.99
	2	20.42	25.1	5.3	72	7.68	5.74
	4	20.43	25.1	5.3	72	8.19	5.99
	6	20.44	25.1	5.7	78		
	8	20.46	25.1	5.5	75		
	10	20.48	25.1	5.5	75		
	12	20.48	25.1	4.5	61		
	14	20.50	25.1	5.4	74		

Time (EST)	Depth (m)	Salinity (o/oo)	Temp (°C)	Dissolved Oxygen (mg/l)	Dissolved Oxygen (% sat)	Light Trans. (%)	Chlorophyll a (µg/l) Total	Chlorophyll a (µg/l) <15 µm
			1 October 1974					
0600	0.5	20.048	17.5	6.94	82		16.9	13.7
	1	20.096	20.5	6.85	85		12.2	12.7
	2	20.052	20.0	7.06	87		14.1	14.8
	4	20.074	20.0	7.14	88		12.3	14.9
	6	20.110	20.1	6.94	86			
	8	20.358	20.2	6.98	86			
	10	23.606	20.2	5.53	70			
	12	23.754	20.3	5.12	65			
	14	24.384	20.3	4.71	59			
0800	0.5	20.727	20.0	7.24	90	42	20.1	19.3
	1	20.723	20.0	7.40	92	27	22.5	21.7
	2	20.712	20.0	7.24	90	9.0	26.1	20.5
	4	20.851	20.0	7.40	92	1.4	26.7	22.3
	6	21.038	20.0	7.30	91			
	8	21.082	20.0	7.08	88			
	10	21.441	20.0	7.12	88			
	12	23.632	20.2	5.54	70			
	14	24.000	20.2	4.84	61			
1000	0.5	20.998	20.6	7.72	97	45	23.8	17.9
	1	21.067	20.6	7.60	96	30	17.2	21.6
	2	21.067	20.5	7.62	96	10	25.0	20.8
	4	21.100	20.6	7.52	95	1.8	27.6	25.1
	6	21.177	20.2	7.70	97	0.2		
	8	21.192	20.2	7.44	94			
	10	21.779	20.2	7.74	97			
	12	22.949	20.8	6.72	86			
	14	24.429	20.8	4.60	59			
1200	0.5	20.351	21.0	8.00	101	49	14.3	17.2
	1	20.409	20.8	8.20	104	33	25.0	27.0
	2	20.533	20.8	7.60	96	13	18.7	18.3
	4	20.983	20.6	7.50	93	1.7	25.3	21.3
	6	21.104	20.2	7.32	91	0.3		
	8	21.364	20.2	7.06	88			
	10	22.140	20.2	6.04	75			
	12	22.735	20.3	5.54	70			
	14	24.119	20.6	4.72	60			

1400	0.5	20.252	20.2	7.60	94	53	20.6	19.8
	1	20.139	20.2	7.94	99	31	18.5	18.9
	2	20.219	20.2	7.70	95	8.3	11.4	15.2
	4	20.694	20.2	6.94	87	1.2	13.5	9.5
	6	20.994	20.2	7.42	93	0.2		
	8	21.261	20.1	7.14	89			
	10	21.871	20.1	6.56	82			
	12	23.042	20.5	5.26	66			
	14	23.743	20.5	4.66	59			
1600	0.5	19.768	21.0	9.64	121	29	21.3	24.5
	1	19.761	21.0	9.40	118	15	27.6	18.5
	2	19.852	21.0	9.04	114	5.4	20.2	18.7
	4	20.107	20.7	7.14	90	0.5	16.8	14.0
	6	20.979	20.2	6.42	80			
	8	22.137	20.2	5.74	71			
	10	22.664	20.2	5.52	69			
	12	23.602	20.6	5.14	65			
	14	24.388	20.8	4.66	60			
1800	0.5	19.794	19.0	9.40	114	40	25.3	14.4
	1	18.823	19.0	7.82	98	23	18.7	19.1
	2	19.939	18.8	8.40	102	6.6	21.7	20.5
	4	20.566	18.8	6.68	81	1.0	15.3	12.3
	6	21.214	18.8	7.22	88	0.1		
	8	21.478	18.8	6.78	83			
	10	21.982	18.8	6.40	78			
	12	23.038	19.2	5.40	67			
	14	23.985	19.2	4.72	59			
2000	0.5	19.954	20.0	7.90	98		12.4	11.7
	1	19.855	20.0	7.74	96		13.8	13.0
	2	19.877	20.0	7.96	98		14.9	12.8
	4	20.774	20.1	7.40	92		10.9	14.9
	6	20.833	20.1	7.50	93			
	8	20.855	20.2	8.00	99			
	10	22.092	20.2	6.50	82			
	12	22.849	20.2	5.80	73			
	14	22.945	20.3	5.70	72			
2200	0.5	20.453	19.9	8.41	105		21.31	21.02
	1	20.811	20.0	7.93	98		25.92	22.60
	2	20.902	19.8	7.46	93		23.90	20.16
	4	21.474	20.0	7.13	88		21.16	19.15
	6	21.802	20.0	6.83	85			
	8	21.897	20.0	6.85	85			
	10	21.897	20.0	6.73	84			
	12	22.328	20.0	6.18	77			
	14	22.709	20.0	5.40	67			

2 October 1974

2400	0.5	20.694	19.8	7.70	96	19.41	15.53
	1	20.661	19.9	7.76	97	19.24	20.42
	2	20.668	19.9	7.70	96	17.05	16.88
	4	20.716	19.9	7.74	96	22.96	23.29
	6	20.683	19.9	7.60	85		
	8	21.199	20.0	6.98	87		
	10	21.628	20.0	6.80	85		
	12	21.934	20.0	6.34	79		
	13.5	23.680	20.2	4.72	60		
0200	0.5	20.391	19.5	7.20	90	13.00	14.43
	1	20.325	19.9	7.18	89	14.26	14.94
	2	20.274	19.9	7.32	91	8.61	13.84
	4	20.300	19.9	7.32	91	16.88	17.05
	6	20.358	19.9	8.40	105		
	8	21.111	20.0	6.94	87		
	10	21.614	20.0	6.22	77		
	12	22.428	20.1	5.55	69		
	14	23.699	20.2	4.70	59		
0400	0.5	20.183	19.7	7.50	93	11.22	13.75
	1	20.099	19.7	8.02	99	8.01	14.01
	2	20.096	19.7	7.52	93	7.00	9.70
	4	20.096	19.7	7.80	96	10.88	13.08
	6	20.081	19.8	7.72	95		
	8	21.236	20.0	6.60	82		
	10	21.904	20.0	6.00	75		
	12	23.346	20.2	4.70	59		
	14	24.548	20.2	4.20	53		
0600	0.5	20.056	19.2	7.70	95	14.85	15.19
	1	20.048	19.5	7.24	89	15.69	14.93
	2	20.110	19.5	7.46	91	8.77	15.19
	4	20.165	19.8	7.28	89	16.03	17.38
	6	20.840	19.9	7.02	86		
	8	21.713	20.0	6.14	76		
	10	21.728	20.0	6.24	78		
	12	22.694	20.1	5.30	67		
	14	23.844	20.2	4.58	58		

0800	0.5	20.420	19.0	7.40	90		18.39	16.37
	1	20.307	19.1	7.50	91		20.45	18.73
	2	20.365	19.3	7.70	94		22.45	17.89
	4	20.409	19.3	7.40	90		19.07	15.86
	6	20.453	19.3	7.60	92			
	8	20.544	19.3	6.96	85			
	10	21.930	19.3	6.20	76			
	12	22.365	19.9	5.62	69			
	14	23.168	20.1	5.10	64			
1000	0.5	21.041	19.1	7.44	91	46	26.83	26.33
	1	21.020	19.1	7.30	89	26	29.03	24.64
	2	21.041	19.1	7.48	91	10	30.55	24.13
	4	21.177	19.1	7.46	91	0.4	27.51	22.78
	6	21.287	19.3	7.44	91			
	8	21.555	19.3	7.30	89			
	10	21.665	19.4	7.08	86			
	12	22.421	19.9	6.14	77			
	14	22.945	20.1	5.14	64			
1200	0.5	21.614	19.0	7.88	96		17.55	28.02
	1	21.510	19.0	7.42	91		28.52	23.80
	2	21.592	19.0	7.50	92		24.64	23.46
	4	21.595	19.1	7.60	93		27.51	22.78
	6	21.566	19.1	7.52	92			
	8	21.540	19.1	7.28	89			
	10	21.581	19.1	7.50	92			
	12	21.603	19.1	7.50	92			
	14	21.665	19.3	7.36	90			
1400	0.5	20.522	19.5	7.82	96		24.30	21.77
	1	20.478	19.5	8.00	98		25.32	23.63
	2	20.486	19.6	7.68	94		21.60	20.76
	4	20.544	19.5	7.78	95		23.12	19.24
	6	20.614	19.8	7.66	94			
	8	21.031	19.9	7.66	95			
	10	22.048	20.0	6.55	82			
	12	22.284	20.1	5.55	69			
	14	23.375	20.2	4.98	63			
1600	0.5	20.271	19.1	7.92	96	51	23.52	25.70
	1	20.271	18.8	8.36	102	29	24.86	22.51
	2	20.263	18.8	8.40	102	8.1	24.69	21.61
	4	20.287	18.9	8.30	101	1.2	22.17	22.00
	6	20.322	19.2	8.16	99	0.2		
	8	20.541	19.2	7.26	88			
	10	21.651	20.0	6.77	84			
	12	22.997	20.1	5.33	67			
	14	23.294	20.2	5.05	64			

Time (EST)	Depth (m)	Salinity (o/oo)	Temp (°C)	Dissolved Oxygen (mg/l)	Dissolved Oxygen (% sat)	Light Trans. (%)	Chlorophyll a (µg/l) Total	Chlorophyll a (µg/l) <15 µm
			13 November 1974					
0600	0.5	22.638	15.2	8.02	91		3.79	2.59
	1	22.627	15.8	7.84	90		2.67	3.75
	2	22.624	15.8	9.10	105		4.43	2.82
	4	22.631	15.8	7.82	90		4.17	3.33
	6	22.646	15.8	8.02	92			
	8	22.638	15.8	7.92	91			
	10	22.627	15.8	8.24	95			
	12	23.427	16.0	7.80	91			
	14	23.580	16.0	7.68	89			
	15.5	23.602	16.0	7.84	91			
0800	0.5	22.638	15.8	7.82	90	53	3.67	3.84
	1	22.642	16.0	8.02	93	41	4.47	2.91
	2	22.650	16.0	7.98	92	11	3.84	3.67
	4	22.661	16.0	7.62	88	2.9	4.13	3.33
	6	22.675	16.0	8.04	93	0.6		
	8	22.683	16.0	8.22	95	0.2		
	10	22.960	16.0	8.08	94			
	12	23.357	16.0	7.64	89			
	14	23.461	16.0	7.92	92			
	15	23.446	16.0	7.50	87			
1000	0.5	22.779	16.0	8.16	95	64	4.60	3.42
	1	22.786	16.0	8.06	94	48	4.97	3.84
	2	22.779	16.0	8.24	96	19	4.55	2.49
	4	22.775	16.0	8.02	93	6.7	5.02	3.54
	6	22.794	16.0	8.02	93	2.4		
	8	22.890	16.0	8.02	93			
	10	23.056	16.0	8.22	95			
	12	23.791	16.1	7.64	89			
	14	24.520	16.2	7.17	83			
	15	24.735	16.2	7.23	84			
1200	0.5	22.660	16.0	8.10	94	49	4.22	4.43
	1	22.661	16.0	8.00	93	40	4.85	3.37
	2	22.657	16.0	7.74	89	20	5.06	4.55
	4	22.620	16.0	7.81	91	7.2	5.27	4.34
	6	22.620	16.0	7.25	84			
	8	22.642	16.0	8.20	95			
	10	22.694	16.0	7.85	91			
	12	22.849	16.0	7.60	88			
	13	22.842	16.0	7.71	89			

1400	0.5	22.502	15.9	7.82	90	57	3.37	2.57
	1	22.502	16.0	7.62	88	34	3.75	2.53
	2	22.505	16.0	7.58	87	20	3.46	2.95
	4	22.524	16.0	8.34	96	7.1	3.79	2.87
	6	22.520	16.0	7.44	86	2.1		
	8	22.598	16.0	7.70	89			
	10	22.746	16.0	7.76	89			
	12	22.897	16.0	7.50	86			
	14	23.985	16.0	7.62	89			
1600	0.5	22.402	15.8	7.52	87	68	3.29	3.04
	1	22.428	15.8	7.44	86	29	3.04	2.53
	2	22.395	15.8	7.98	92	14	3.16	2.53
	4	22.461	15.8	7.86	91	2.5	3.21	2.57
	6	22.446	15.8	7.13	82	0.8		
	8	22.653	15.8	7.50	87			
	10	22.683	15.9	8.32	96			
	12	23.060	15.9	8.22	96			
	14	23.083	16.0	8.20	96			
1800	0.5	22.454	14.8	8.02	92		2.99	2.28
	1	22.446	15.2	8.32	95		2.78	2.53
	2	22.432	15.5	7.96	92		2.91	2.28
	4	22.491	15.5	7.52	86		2.70	2.49
	6	22.727	15.5	7.62	87			
	8	22.834	15.8	7.82	89			
	10	22.849	15.8	7.62	87			
	12	23.405	15.8	7.64	88			
	14	23.669	15.8	7.42	86			
2000	0.5	22.528	15.5	7.52	86			
	1	22.505	15.5	7.68	88			
	2	22.513	15.6	7.66	88			
	4	22.528	15.6	7.64	87			
	6	22.539	15.6	8.02	92			
	8	22.605	15.8	7.82	89			
	10	23.457	15.8	7.58	88			
	12	23.557	15.9	7.52	87			
	14	23.609	15.9	7.52	87			
2200	0.5	22.635	15.5	7.66	88			
	1	22.620	15.5	7.77	89			
	2	22.687	15.5	7.82	90			
	4	22.820	15.7	8.05	94			
	6	22.868	15.7	7.82	91			
	8	23.112	15.7	7.86	91			
	10	23.149	15.8	7.81	91			
	12	23.197	15.8	7.54	87			
	14	24.335	16.0	7.73	90			

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2400	0.5	22.687	15.1	7.84	89	2.06	2.19
	1	22.650	15.1	7.92	90	1.74	1.92
	2	22.672	15.2	7.92	89	1.05	1.68
	4	22.635	15.2	7.86	89	2.10	2.39
	6	22.653	15.2	7.72	87		
	8	22.635	15.2	7.84	89		
	10	22.635	15.2	7.99	90		
	12	22.646	15.2	7.64	86		
	14	23.272	15.2	7.52	85		
0200	0.5	22.432	15.5	7.72	89	1.93	1.73
	1	22.417	15.5	7.68	88	1.93	0.95
	2	22.428	15.7	7.78	89	1.66	1.45
	4	22.421	15.8	7.64	88	1.94	1.67
	6	22.424	15.8	7.60	87		
	8	22.905	15.9	7.44	86		
	10	23.754	16.0	7.58	88		
	12	24.578	16.0	7.23	85		
	14	24.776	16.1	7.03	82		
0400	0.5	22.398	15.3	7.52	86	1.37	1.71
	1	22.354	15.4	7.82	89	1.10	1.08
	2	22.328	15.4	7.62	87	1.10	1.71
	4	22.347	15.3	7.60	87	1.40	1.38
	6	22.816	15.3	8.00	92		
	8	22.809	15.3	7.86	90		
	10	23.064	15.5	7.66	88		
	12	23.208	15.7	7.27	84		
	14	25.173	15.8	7.01	82		
0600	0.5	22.409	15.0	7.84	89	1.87	1.64
	1	22.413	15.0	7.78	88	1.70	1.70
	2	22.395	15.1	7.46	84	1.81	2.42
	4	22.432	15.2	7.52	85	2.06	1.24
	6	22.616	15.3	7.52	85		
	8	23.001	15.5	8.00	93		
	10	23.309	15.8	7.56	88		
	12	23.461	15.8	7.66	89		
	14	23.784	15.9	7.42	86		
0800	0.5	22.505	15.8	7.92	91		
	1	22.483	15.7	7.92	91		
	2	22.487	15.7	7.86	91		
	4	22.509	15.7	7.86	91		
	6	22.568	15.8	7.84	90		
	8	22.524	15.8	7.62	88		
	10	23.097	15.8	7.66	88		
	12	23.658	15.9	7.78	91		
	14	23.728	16.0	7.56	88		
	16	23.758	15.9	7.78	91		

1000	0.5	22.572	16.0	7.72	89	50	2.32	1.94
	1	22.568	16.0	7.72	89	38	2.00	1.86
	2	22.568	16.0	7.74	89	24	2.02	1.81
	4	22.664	16.0	7.96	92	6.3	2.87	2.07
	6	22.908	15.8	7.98	93	4.0		
	8	22.920	15.8	8.16	95			
	10	23.253	15.9	7.78	91			
	12	23.948	15.9	7.84	91			
	14	24.597	16.1	7.65	90			
	16	25.203	16.3	7.42	88			
1200	0.5	22.568	16.0	7.86	91		2.06	1.44
	1	22.565	15.8	7.92	92		3.00	2.41
	2	22.553	15.8	8.02	93		2.42	1.90
	4	22.561	15.9	7.92	92		2.26	2.28
	6	22.572	15.9	8.00	93			
	8	22.868	15.9	7.80	91			
	10	24.059	15.9	7.72	90			
	12	24.223	15.9	7.68	90			
	14	24.784	16.0	7.64	90			
	15.5	24.956	16.0	7.64	90			
1400	0.5	22.472	15.8	8.02	92	55	2.79	2.28
	1	22.472	15.9	8.12	93	37	3.08	2.53
	2	22.457	15.9	8.02	92	23	3.76	4.14
	4	22.461	15.9	8.02	92	6.0	3.76	3.25
	6	22.535	15.9	8.02	92	1.1		
	8	22.624	15.9	7.52	87			
	10	23.056	15.9	7.86	91			
	12	23.769	15.8	7.52	88			
	14	24.276	15.9	7.60	88			
1600	0.5	22.203	15.8	7.84	90		2.30	3.04
	1	22.203	15.8	7.60	87		2.79	2.32
	2	22.207	15.8	7.68	88		3.71	3.50
	4	22.299	15.8	7.98	92		3.29	2.83
	6	22.428	15.8	7.98	92			
	8	23.019	15.9	7.94	92			
	10	23.702	15.9	7.86	92			
	12	24.660	16.0	7.26	85			
	14	25.027	16.1	7.26	85			
	16	25.218	16.2	7.62	89			

VITA

Leonard William Haas

Born in Cincinnati, Ohio, 15 November 1944. Graduated from Camp Hill High School, Camp Hill, Pennsylvania in June 1962; from Dartmouth College, Hanover, New Hampshire in June 1966 with a major in biology; and from the University of Rhode Island, Kingston, Rhode Island with an M.S. degree in zoology.

In September 1968, I entered the School of Marine Sciences of the College of William and Mary in Virginia to pursue a Ph.D. in Marine Science. From that date to the present I have been the recipient of a graduate assistantship in the Department of Environmental Physiology, Virginia Institute of Marine Science (VIMS), except for the period May 1972 through January 1975 when I was employed as a Marine Scientist B at VIMS.